THE CLOACAL COMPLEX IN *PSEUDOCORDYLUS MELANOTUS* and in *CORDYLUS CORDYLUS* (SAURIA: CORDYLIDAE)

by

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VERKLARING

Ek, die ondergetekende, verklaar hiermee dat die werk in hierdie tesis vervat, my eie oorspronklike werk is wat nog nie vantevore in die geheel of gedeeltelik by enige ander universiteit ter verkryging van 'n graad voorgelê is nie.

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CONTENTS

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ABSTRACT

The cloacal anatomy of *Pseudocordylus melanotus* and *Cordylus cordylus* was examined macroscopically and by light microscopy. The cloacal subdivisions are the coprodaeum, the urodaeum and the proctodaeum. Both the coprodaeum and the proctodaeum typically start as sphincter-like structures. However, the border between the coprodaeum and urodaeum is not well delimited. The start of the cloaca from the intestine is marked by a change in epithelium, from consisting of columnar and goblet cells to a columnar epithelium consisting of mucous secreting cells. The urinary bladder extends ventrally from the coprodaeum-urodaeum part of the cloaca and is connected with it by means of a stalk. The most striking sexual differences in the cloacal complex anatomy are associated with the urodaeum. Females possess anterior urodaeal limbs which are reduced in males. The urodaeum of females exhibits tall dorsal folds which are reduced or absent in males. In females the urogenital ducts (uteri and ureters) open separately through the dorsal wall of the cloaca - the uteri in the anterior part of the urodaeum and the ureters in the coprodaeum-urodaeum cavity. In males the vas deferens and ureter on each side coalesce to open conjointly into the coprodaeum-urodaeum cavity by means of a short ductus urogenitalis. This junction is in approximately the same position as the junction of the ureter with the cloaca in females. Two types of cloacal glands were observed in the cordylid species examined. Dorsal and ventral glands were found laterally on both sides of the proctodaeum in males and females, but were more pronounced in males. Urodaeal glands were observed only in the urodaeal walls of females. Pronounced seasonal variation was observed in the secretory activity of the luminal lining of the urodaeum of all females examined (both species) and in the urodaeal gland epithelia of one *C. cordylus* female. Neither of the cordylid species show any seasonal variation in the structure of the dorsal and ventral

glands in any of the sexes. Little variation in cloacal anatomy occurred between the two cordylid species. However, the urodaeal limbs in most of the *P.melanotus* females examined, stretch further anteriorly than in *C.cordylus*. The intraspecific variations observed were primarily associated with the relative position of the coprodaeum-urodaeum junction as well as the position of the junction between the urinary bladder stalk and the cloaca (coprodaeum and/or urodaeum). The relatively thick connective tissue ventral to the proctodaeum may serve as 'gliding surface' when the cloaca is pushed backwards during copulation. If sperm are stored in the cordylid species examined, it would probably be in the vas deferens of the males.

UITTREKSEL

Die kloakale anatomie van *Pseudocordylus melanotus* en *Cordylus cordylus* is makroskopies en histologies ondersoek. Die drie onderafdelings van die kloaka is die koprodeum, die urodeum en die proktodeum. Beide die koprodeum en proktodeum begin tipies as sfinkteragtige strukture. Die oorgang vanaf die intestinum na die proktodeum word gekenmerk deur 'n verandering in die tipe epiteelselle - vanaf die kolomepiteel van die intestinum wat bestaan uit kolom- en bekervormige selle na 'n kolomepiteel wat slegs uit slym-sekreterende selle bestaan. Die grens tussen die koprodeum en die urodeum is nie duidelik afgebaken nie. Die urinêre blaassteeljie is 'n ventrale uitsakking van die koprodaeum-urodeum gedeelte en verbind die urinêre blaas met die kloaka. Die grootste verskil in kloakale anatomie tussen mannetjies en wyfies word aangetref in die urodeum. In wyfies verleng die urodaeum as twee 'bene' na voor, dorsaal van die koprodeum, terwyl urodeale verlengings ('bene') na voor in mannetjies afwesig is. In teenstelling met die urodeum van die wyfie, wat dorsaal redelik gevou is, is die wand van die mannetjie net effens gevou. In wyfies open die urogenitale buise (uteri en ureters) apart in die kloaka - die uteri in die voorste urodeum gedeelte en die ureters meer na agter, in die koprodeum-urodeum holte. In mannetjies sluit die vas deferens en die ureter aan beide kante bymekaar aan, voordat dit deur middel van 'n gemeenskaplike opening in die koprodeum-urodeum holte open. Laasgenoemde urogenitale opening is omtrent in dieselfde posisie as die ureters se aansluiting in die kloaka van die wyfie. Twee tipes kloakale kliere is in die twee gordelakkedis species wat ondersoek is, aangetref. Dorsale- en ventrale kliere, wat in mannetjies meer uitgespreke is, word dorso- en ventro-lateraal aan beide kante van die proktodeum aangetref. Die defnitiewe funksies van bogenoemde kliere is nog nie bekend nie, alhoewel daar heelwat hieroor gespekuleer word. Urodaeale kliere, wat met die wande van die urodeum geassosieerd is, word net in wyfies aangetref. Seisoenale

variasie is waargeneem in die sekreterende aktiwiteit van die urodeale epiteel en ook van die urodaeale kliere van een *C. cordylus* wyfie. Hierdie seisoenale variasie is moontlik geassosieerd met die voortplantingsiklus van die dier. Geen seisoenale variasie is in die struktuur van die dorsale- en ventrale kliere aangetref nie. Die kloakale anatomie van die twee gordelakkedis species stem baie ooreen. Die urodeale gedeelte in die meeste *P. melanotus* wyfies wat ondersoek is, strek egter verder na voor as in die geval van *C. cordylus*. Die waargenome intraspesifieke variasies staan veral in verband met die posisie van die urinêre blaassteeltjie se aansluiting met die koprodeum, urodeum of albei. Die posisie van die koprodeum-urodeum-aansluiting kan ook binne dieselfde spesie varieer. Die relatief dik bindweefsel, ventraal van die koprodeum kan moontlik as 'glyvlak' dien wanneer die kloaka agtertoe gedruk word, tydens kopulasie.

CHAPTER 1

INTRODUCTION

1.1. BACKGROUND

A comparative study of the reproductive tracts of vertebrates by Lereboullet (1851) brought the composition of the saurian cloaca to attention (Gabe and Saint Girons 1965). Gadow (1887) was the first to describe the basic cloacal anatomy of lizards and snakes. He described the cloacal region with three subdivisions: the coprodaeum which joins the cloaca with the intestine; the urodaeum which receives the genital and urinary products; and the proctodaeum which leads to the exterior. He also mentioned the proctodaeum to be ectodermal and the urodaeum and coprodaeum to be endodermal. The majority of authors after 1900 conserved the subdivisions proposed by Gadow, but found it difficult to define the exact borders of the different segments (Gabe and Saint Girons 1965). Work done by Fleischman and his students (1902), notes of Woepke (1931) and publications of Gerhardt (1937) are other important early studies which included descriptions of the cloacal anatomy of lepidosaurians.

The most extensive and detailed study of the lepidosaurian cloaca is that by Gabe and Saint Girons (1965), who included representatives of 23 families. Relatively few snakes and only two species of amphibaenians were, however, included. The most complete study dealing specifically with glands of the cloacal region in lizards and snakes, is that of Whiting (1969). Whiting (op cit.) established that glands associated with the cloaca are found in all the major groups of Sauria and Serpentes and she reported 11 types of glands in the cloacal region of various squamates.

Work done on the cloacal anatomy of lizards has shown that there are several differences between the sexes in both the gross- and microanatomy of the cloaca (Gabe and Saint Girons 1965). Furthermore, seasonal variation in

cloacal anatomy, which is correlated with the reproductive cycle, has been reported for many species (Gabe and Saint Girons 1965; Trauth, Cooper Jr., Vitt and Perril 1987). Changes associated with different stages of sexual maturity have also been reported (Gabe and Saint Girons 1965; Trauth *et al.* 1987).

1.2. RATIONALE

The lizard family Cordylidae (sensu Lang 1991) is endemic to Africa and to date has received little attention from researchers. The family is comprised of four genera, viz. *Chamaesaura*, *Cordylus*, *Pseudocordylus* and *Platysaurus*, the phylogenetic relationships of which were recently established (Lang 1991). Characters of soft anatomy used in the above cladistic analysis notably excluded characters of the cloacal complex, simply because no information was available for any of the species of which the family is comprised. Data are, however, available for the family Gerrhosauridae, the sister group of the Cordylidae, as well as for the families Lacertidae, Scincidae and Teiidae, which together with the former two, constitute the infraorder Scincomorpha. For a complete phylogenetic perspective of the anatomy of the cloacal complex within the infraorder, data for the Cordylidae are needed.

Lang (1991) proposed that the genus *Chamaesaura* occupies the basal position in the Cordylidae clade, followed by *Cordylus* and *Pseudocordylus*, in that order, and with *Platysaurus* the most derived genus. In a phylogenetic analysis of the family Cordylidae, using species as operational units, preliminary studies of Herselman (1991) and Herselman, Mouton and Van Wyk (1992) showed that *Platysaurus* is embedded within *Pseudocordylus* and *Pseudocordylus* within *Cordylus*. This means that *Pseudocordylus* and *Cordylus* are both paraphyletic groups and that the formal classification for the family will have to be changed to obtain monophyletic taxa. Before resorting to such drastic measures, the proposed cladistic hypothesis of Herselman (1991) needs to be

corroborated. To achieve this, additional character sets are needed and the cloacal complex may provide information for such purposes.

It has long been suspected that cloacal secretions may be important to intraspecific communication in saurian species (Simon 1983). Cooper *et al.* (1986) established that the urodaeal glands in females stimulates courtship by conspecific males. The taxonomic distribution of pheromonal communication is largely unknown (Cooper and Trauth 1992) and information on cloacal glands of the family Cordylidae is non-existent. Interest in aspects of reproduction, as well as the social structure of cordylid species has increased considerably over the past years (Burrage 1974; Van Wyk 1983, 1989, 1991, 1992; Flemming and Van Wyk 1992; Flemming 1993a b; Mouton and Van Wyk 1993a) and as the cloacal glands are seemingly closely involved in these aspects, information on these glands are needed.

1.3. ANIMALS INVESTIGATED

The Drakensberg crag lizard, *Pseudocordylus melanotus* Figure 1(a) and the Cape girdled lizard, *Cordylus cordylus* Figure 1(b) were selected as representative species for the investigation of the cloacal anatomy in the family Cordylidae. Their selection was based on the availability of sufficient material in the museum collection, as well as the availability of data on reproduction (Flemming 1993a,b; Jacobs unpublished data) and social behaviour (Burrage 1974; Mouton and Van Wyk 1993a). Furthermore, these two species follow different reproductive strategies which make them ideal for comparison of the urodaeal gland cycles (Jacobs unpublished data; Flemming 1993a,b).

Both species are heliothermic baskers which follow a sit-and-wait feeding strategy (Burrage 1974; Mouton and Van Wyk 1993a,b). They are both insectivorous and their diets include a wide variety of prey items, from small beetles to flying insects (Branch 1988; Mouton and Van Wyk 1993b).

Pseudocordylus melanotus occurs in dense colonies where the social structure is one of territorial polygyny (Griffiths unpublished data; Mouton and Van Wyk 1993a). This species also displays a high degree of sexual dimorphism in body size, head size and coloration which is ascribed to the combined influences of sexual selection and differential energy allocation by females (Mouton and Van Wyk 1993a). In this species active femoral and generation glands occur in males only (Mouton and Van Wyk op cit.). The function of these glands are still unknown but pheromonal communication is suspected (Van Wyk and Mouton 1992).

Cordylus cordylus also occurs in dense colonies, but unlike in *P. melanotus*, females are also territorial and the social structure is apparently a monogamous one (Burrage 1974). No apparent sexual dimorphism in size and coloration occurs and both males and females have well-developed femoral glands (Branch 1988). Generation glands are always present in males, but their presence in females is apparently determined by climatic parameters (Jacobs unpublished data).

C. cordylus has an extensive range in southern Africa and occupies the coastal regions of the Cape from Saldanha bay in the West to East London in the east (FitzSimons 1943; Loveridge 1944; Branch 1988a). In the east it also reaches further inland as far as the southern Orange Free State (De Waal 1978). *P.melanotus* ranges from the Amatola Mountains in the eastern Cape to the Transvaal Drakensberg, extending also onto the Orange Free State Highland (De Waal 1978; Branch 1988a). The taxonomy of *P. melanotus* is confused. Three subspecies are currently recognised, but these are not well delimited (Branch 1988b). The material investigated in this study can be assigned to the subspecies *subviridis*, but because of the unclear taxonomic status, subsequent reference will be to species only.

Figure 1. (a) *Cordylus cordylus*
(b) *Pseudocordylus melanotus*

1.4 REPRODUCTIVE CYCLE

Reptiles are noteworthy among amniotes for displaying both oviparous and viviparous modes of reproduction (Bradshaw 1986). Both *Pseudocordylus melanotus* and *Cordylus cordylus* exhibit a viviparous mode of reproduction. Temperate zone reptiles exhibit distinct patterns of seasonal reproductive activity (Fitch 1970; Duval, Guillette Jr. and Jones 1982; Licht 1984; Lofts 1985). The most common reproductive pattern in temperate lizards, which is dominant in those species exhibiting oviparity (Fitch 1970), is that in which males and females exhibit spring gonadogenesis, with subsequent courtship, mating and oviposition. However, in many viviparous lizards gametogenesis, courtship and mating occur in fall, with parturition during early spring (Pearsons 1954; Crisp 1964; Goldberg 1970; Callard, Chan, Anderson Potts 1972; Ballinger 1973; Guillette 1983; Ortega and Barbault 1984; Guillette and Casas-Andreu 1987). There are, however, viviparous temperate lizards which exhibit spring reproductive activity (Miller 1951; Vitt 1973; Steward 1979, 1985; Xavier 1982). Patterns also exist in which male and female reproductive activity occurs asynchronously, for example *Sceloporus grammiccus microlepidotus* (Guillette and Casas-Andreu 1980) and *Sceloporus formosus* (Guillette and Sullivan 1985) in which maximum testicular activity occurs in spring whereas ovarian activity (vitellogenesis and ovulation) occurs in autumn. The South-African lizards, *Cordylus polyzonus* and *C. giganteus* both exhibit autumn/winter vitellogenesis, ovulate in late winter-spring and give birth in summer (Van Wyk 1989, 1990; Flemming and Van Wyk 1992). In *C. polyzonus* the testicular activity of males reaches a peak in June and July (winter) with ovulation of the females in October (spring).

In *Pseudocordylus melanotus* reproductive activity of the males and females is asynchronous, with spermiogenesis in males reaching a peak in autumn and ovulation in females occuring in early spring (Flemming 1993a). Griffiths (unpublished data) established that mating in this species occurs in

autumn. Vitellogenesis in females, however, starts in autumn, while the young (1-4) are born in late summer (Flemming 1993a). In contrast to *P. melanotus* the reproductive cycles of male and female *Cordylus cordylus* are more synchronised, with maximum testicular activity in males in the late winter/early spring and ovulation in females occuring in early spring with parturition in summer (Jacobs unpublished data).

1.5. AIMS

In both species the gross anatomy and the microanatomy of the cloaca of both sexes in different reproductive stages were examined with the following aims in mind:

1. To provide a detailed anatomical description of the cloacal complex for the two species examined.
2. To describe sexual differences in cloacal anatomy in the two species.
3. To establish whether seasonal variation in cloacal structure occurs in the two species.
4. To compare the cloacal anatomy of *P. melanotus* and *C. cordylus* in order to obtain an additional character set which can be used in the refinement of cladistic relationships within the family.
5. To compare the cloacal anatomy of the two cordylid species examined with other reptile species, for which data are available, in order to obtain a phylogenetic and a functional perspective of cloacal morphology in the Sauria.

CHAPTER 2

MATERIALS AND METHODS

2.1 Materials

Material of *Cordylus cordylus* and *Pseudocordylus melanotus* were obtained from the John Ellerman Museum, University of Stellenbosch. Specimens were selected to be representative of at least two stages in the reproductive cycle. Female reproductive condition was determined using as criteria the collection date, presence of oviductal eggs, size and appearance of ovarian follicles. Using these criteria, I distinguished three primary conditions- early vitellogenic, vitellogenic and gravid. The relative size of the testes (small or enlarged) in males was used to categorize males as either spermatogenic active or not. Information on reproductive stage, date of collection and sex of the animals used in this study are listed in Table 1 and 2. All the Museum material were initially fixed in 10 % formalin and subsequently preserved in 70 % alcohol.

2.2 Gross anatomy

For determining the gross anatomy, the cloacal complexes of the lizards along with the urogenital tracts, kidneys and lower intestine were exised before it was examined with a stereo-microscope.

2.3 Microanatomy

The cloacal complex along with portions of the kidneys, urogenital tracts and lower intestine were exised from the body of the lizard and placed into vials of 70% ethanol. Standard histological techniques were used to prepare the tissues for examination by light microscopy (Humason 1979). The procedures included dehydration in ethanol, clearing in xylene or toluene and embedding in paraffin wax. Transverse sections (10.m) were serially cut with a rotary microtome and

stained with Azocarmyn-B and azaan (Mallory's triple stain). Cloacal general terminology is that of Hardy and Cole (1981) and Whiting (1969).

Table 1. Stages of reproductivity and date of collection of *Cordylus cordylus* specimens examined.

	Lizard ref.no.	Sex	Collection date	Reproductive stage
Gross anatomy-	JEM 1367	F	23.01.84	V
	JEM 42	M	18.06.83	t
Micro= anatomy-	JEM 423	F	2.12 83	G
	JEM 430	F	22.01.84	G
	JEM 1364	F	09.11.85	G
	JEM 1510	F	27.04.86	V
	JEM 46	F	16.07.83	V
	JEM 165	F	26.09.83	A-V
	JEM 352	M	07.12.83	t
	JEM 356	M	07.12.83	t
	JEM 30	M	20.03.83	Tt
	JEM 32	M	20.03.83	Tt
	JEM 47	M	16.07.83	T

F=female; M=male; G=gravid; T=enlarged testis; t=small testis; Tt=slightly enlarged testis; V=vitellogenic, A-v=advanced vitellogenic, JEM=John Ellerman Museum.

Table 2. Stages of reproductivity and date of collection of *Pseudocordylus melanotus* specimens examined.

	Lizard ref. no.	Sex	Collection date	reproductive stage
Gross anatomy	JEM 2397	F	25.01.92	V
	JEM 2435	M	03.10.91	t
Micro= anatomy	JEM 2365	F	01.10.91	G
	JEM 2368	F	01.10.91	G
	JEM 2618	F	25.01.91	V
	JEM 2438	M	02.10.91	T
	JEM 2456	M	04.12.91	t
	JEM 2609	M	25.01.92	t

F=female; M=male; G=gravid; T=enlarged testis; t=small testis; V=vitellogenic; JEM=John Ellerman Museum.

CHAPTER 3

ANATOMY OF THE CLOACAL COMPLEX OF *PSEUDOCORDYLUS MELANOTUS*.

3.1. FEMALE

3.1.1. Gross anatomy (see Figure 2)

Three cloacal divisions can be identified, namely, the coprodaeum, the urodaeum and the proctodaeum. Dorsally the cloacal compiex is shielded by the kidneys. When the kidneys are removed the urodaeum is visible as a dorsal bulge of the cloaca. The urodaeum extends anteriorly and is divided into two urodaeal limbs which locate positions dorso-lateral to the coprodaeum. The intestine leads to the coprodaeum and the proctodaeum to the exterior. Where the urodaeum joins the coprodaeum, a common cavity (coprodaeum-urodaeum cavity) is formed which leads to the proctodaeum posteriorly. The urinary bladder stalk is a ventral evagination of the cloaca which connects the urinary bladder with the cloaca in the coprodaeum-urodaeum region. The uteri (oviducts) pass ventral to the kidneys and open into the dorsal wall of the urodaeum. The ureters run posteriorly over the ventral surface of the kidneys and open into the coprodaeum-urodaeum cavity.

3.1.2. Microanatomy

To simplify description and discussion of the microanatomy, the cloacal complex was arbitrarily divided into three regions (see Figure 2). Figures 3 - 22 represent anterior to posterior transverse sections of the cloacal complex of a *P.melanotus* female (JEM 2618, collected during late summer, reproductive condition: early vitellogenic). Included also are variations as encountered in other female specimens examined.

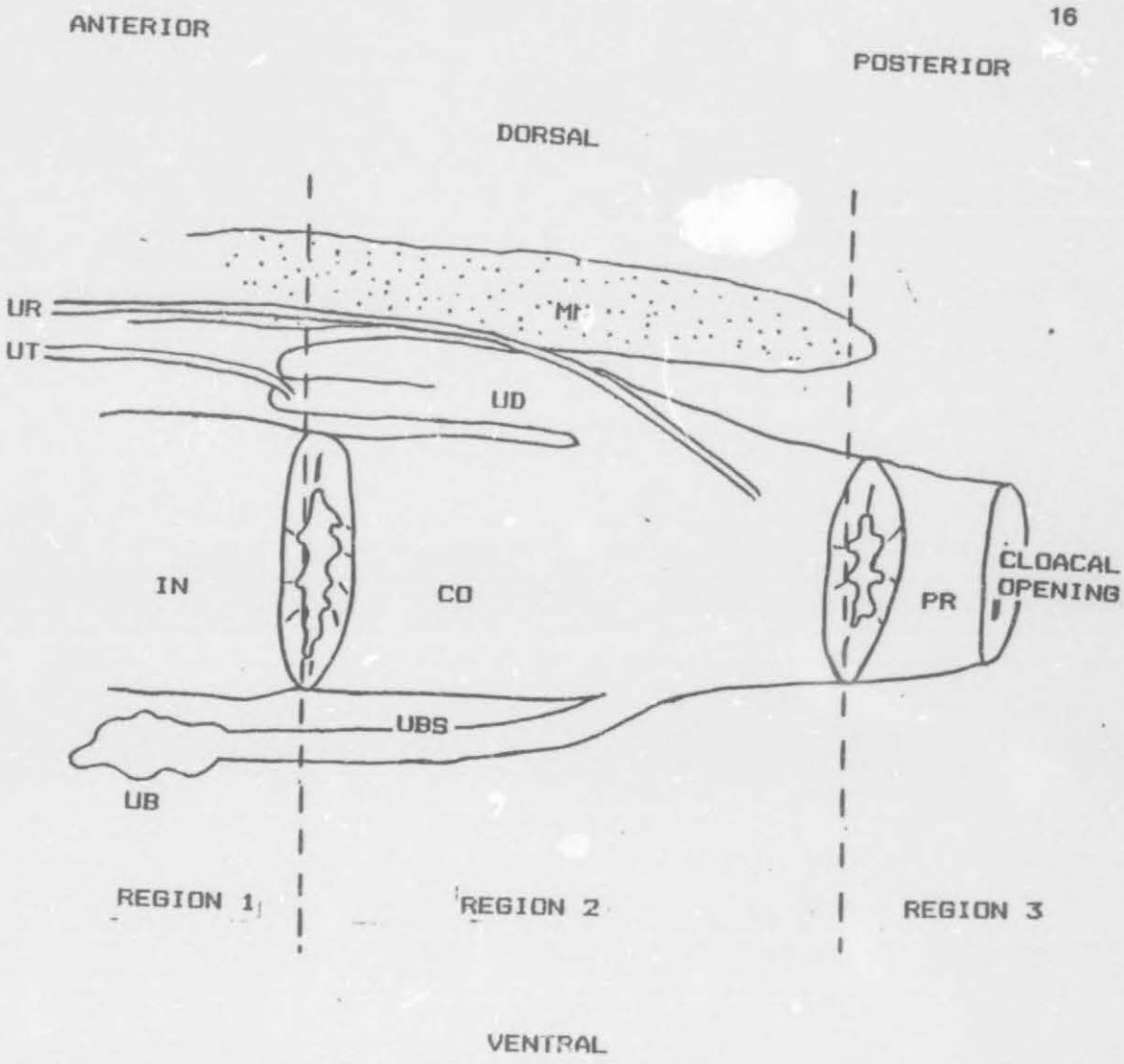

Figure 2. Diagrammatic representation of the cloacal complex of a female *P. melanotus*.
CO=coprodaeum; IN=intestine; MN= metanephros; UB=urinary bladder; UBS=urinary bladder stalk; UD=urodaeum; UR=ureter; UT=uteri; PR=proctodaeum.

3.1.2.1. **Region 1** (see Figure 2)

This region encompasses the terminal part of the intestine, the anterior urodaeal limbs, the urogenital ducts (uteri and ureters), the urinary bladder and part of the urinary bladder stalk.

At the level of Figure 3 the intestine has a more or less ventro-medial position with two dorso-laterally located uteri and a ventro-medially located urinary bladder stalk. In a position dorsal to the uteri are the ureters. Dorsal to the intestine and medial to the uteri, the urodaeum is evident as two anterior urodaeal limbs. Prominent groups of longitudinal smooth muscle fibres are evident dorso-medially to the intestine.

Intestine (Figure 4)

The intestine epithelium is folded and consists of columnar cells with goblet cells scattered among them. The epithelium shows seasonal variation in height, which seems to be correlated with the reproductive condition of the animal (see section on seasonal variation). The layer of connective tissue (lamina propria), which underlies the intestine epithelium, is vascularized and extends into the luminal folds. Together, the lamina propria and the epithelium comprise the mucosa of the intestine. External to the lamina propria are an inner- and an outer muscularis. The inner muscularis consists of two thin smooth muscle layers of which the orientation is primarily circular. At intervals some longitudinal smooth muscle fibres can be seen adjacent to the inner circular muscle fibre layer. The inner muscle layer of the inner muscularis also extends into the luminal folds of the intestine and is separated from the outer muscle layer by vascularized connective tissue. The outer muscularis consists of groups of longitudinal smooth muscle fibres. The inner and outer muscularis are separated from each other by vascularized connective tissue which contains more enlarged blood vessels in the lateral areas. The serosa layer, external to the outer

muscularis, is not well defined and consists of a thin layer of vascularized connective tissue.

Urinary bladder stalk

Anterior part (Figure 5).

The wall of the urinary bladder stalk consists of three layers: a mucosa layer, a muscularis layer and a serosa layer. The mucosa exposes luminal folds and is marked by an inner ciliated pseudostratified columnar epithelium and an underlying layer of loose connective tissue (lamina propria). Some unciliated, mucous secreting cells occur among the ciliated epithelial cells. Basal bodies stained intensively in the ciliated areas. Blood vessels and lymphatic vessels are found in the lamina propria. Some groups of longitudinal smooth muscle fibres, which represent the muscularis mucosa, are embedded in the lamina propria. These longitudinal muscle bundles (muscularis mucosa) are more concentrated on the ventral side of the urinary bladder stalk, especially ventro-medially. The muscularis layer is located external to the lamina propria and in this region consists largely of circularly arranged smooth muscle fibres. The serosa layer external to the muscularis, contains an abundant supply of blood vessels.

Urogenital ducts

Uteri (Figure 6) - The uteri are lined with columnar epithelia which primarily consist of ciliated cells. Tall folds (plicae) extend into the uterus lumen. Cripts are evident in the columnar ciliated epithelium of the plicae. The connective tissue (lamina propria), which underlies the uterus epithelium, extends into the luminal folds. External to the lamina propria, is a relatively thick layer of circularly arranged smooth muscle fibres. Some longitudinally arranged smooth muscle groups were found to be present external to the circularly arranged smooth muscle fibres in some areas.

Ureters (Figure 7) - In this region the ureters locate positions dorso-medial to the uteri and are lined with low simple cubical to columnar epithelia, consisting of cells with basal spheric nuclei.

Urodaeum (anterior urodaeal limbs) (Figure 8)

In this region the urodaeum is evident as two dorso-lateral urodaeal limbs (see Figure 3). The urodaeal limbs expose horseshoe-shaped lumina, lined with columnar stratified epithelia (2-7 layers), which consist of apical mucous secreting cells. The luminal lining of the urodaeum shows seasonal variation, which is correlated with the reproductive cycle (see section on seasonal variation). The dorsal wall of the urodaeum is thicker than the ventral one. Urodaeal glands occur in the walls of the urodaeal limbs. These glands are of the branched, tubular exocrine type and contains mucous secreting cells. The nuclei of these glands are round and exhibit basal positions. A relatively thin layer of circularly arranged smooth muscle fibres are present in the ventral walls of the urodaeal limbs. Protozoan parasites are abundant in the epithelium of the urodaeum and are also present in the epithelia of the urodaeal glands.

4.1.2.2. **Region 2** (see figure 2)

This region includes the coprodaeum, the urodaeum, the urinary bladder stalk and the ureters. The ureters and the urinary bladder stalk join the cloaca in this region.

Coprodaeum

At the level of Figure 9 the coprodaeum is evident as a sphincter-like structure. The epithelium of the intestine has changed from a tall pseudostratified epithelium, consisting of columnar and goblet cells, to the columnar pseudostratified epithelium of the coprodaeum which consists of

columnar mucous secreting cells (Figure 10). The epithelial cells of the coprodaeum contains basal nuclei.

The connective tissue layer which underlies the coprodaeum epithelium, is followed by the inner- and outer muscularis as described for the intestine. However, the inner muscularis of the coprodaeum is better developed than the inner muscularis of the intestine. Due to the folding of the coprodaeum wall it is difficult to define the borders of the circular or longitudinal smooth muscle fibre layers in the inner muscularis in this specimen. However, in the other specimens examined the inner muscularis is primarily comprised of circularly arranged smooth muscle fibres, with some groups of longitudinal smooth muscle fibres occurring in some areas (see Figure 14). Longitudinal muscle fibre groups are more prominent in the lateral regions. The outer muscularis (as was described for the intestine) consists of longitudinal smooth muscle fibre groups which are restricted to locations lateral to the coprodaeum. Protozoan parasites are visible in the dorsal coprodaeum epithelium, nearest to the urodaeum. A common wall, which primarily consists of circularly arranged smooth muscle fibres, exists between the coprodaeum and the urodaeum.

Urodaeum

In this region the anterior urodaeal cavities have coalesced to form the common urodaeal cavity (Figure 9). An abundant supply of blood vessels are evident in the dorsal wall of the urodaeum. As described for the urodaeal limbs in Region 1, the dorsal wall of the urodaeum in this region is thicker than the ventral wall and also exhibits taller folds than the ventral one. The urodaeal glands are restricted to the ventral wall of the urodaeum. Posteriorly, anterior to the urinary bladder stalk junction with the cloaca, a passageway is formed between the coprodaeum and the urodaeum (Figure 11). The urodaeum extends posteriorly, ventral to the proctodaeum while the junction between the two

cloacal divisions enlarges until one cavity is formed, the coprodaeum-urodaeum cavity (Figure 16).

Urinary bladder stalk

Posterior part (Figure 12) - The dorsal muscularis of the urinary bladder stalk is now more prominent than in the anterior part of the urinary bladder stalk, described in Region 1 (see Figure 9) and is separated from the inner muscularis of the coprdaeum by means of a thin layer of connective tissue. The outer muscularis of the coprodaeum is consolidated with the ventral muscularis of the urinary bladder stalk. The urinary bladder stalk still has a pseudostratified columnar epithelium, but in contrast with the anterior part of the stalk (Region 1), where the epithelium primarily consists of ciliated cells, the epithelium of the urinary bladder stalk, near its junction with the cloaca, primarily consists of unciliated mucous secreting cells. In contrast with the situation observed in Region 1 where the ventral muscularis primarily consists of circularly arranged muscle fibres, the ventral muscularis of the urinary bladder stalk now mainly consists of longitudinal muscle fibre groups. The muscularis mucosa observed in Region 1 is now absent. Approximately 430 μ.n posterior to the junction between the urodaeum and the coprodaeum, the urinary bladder stalk opens into the urodaeum-coprodaeum cavity (Figure 13). This opening is located lateral to the dorsal inner muscularis of the coprodaeum. It is difficult to distinguish between the columnar pseudostratified epithelium of the urinary bladder stalk and that of the coprodaeum. The urinary bladder stalk extends posteriorly, ventral to the coprodaeum-urodaeum cavity with which it remains in connection. Posteriorly, the posteriorly extended ventral inner muscularis, which separates the lumina of the urinary bladder stalk and that of the coprodaeum-urodaeum cavity, is lacking, and result in a enlarged coprodaeum-urodaeum cavity. The urinary bladder stalk junction with the cloaca can also be at more or less the same level or just anterior to the coprodaeum-urodaeum junction, as was found

in another specimen examined (Figure 14). In the latter specimen the lumen of the urinary bladder stalk extends dorsally, lateral to the inner muscularis of the coprodaeum to find connection with the urodaeum, just anterior to where the urinary bladder stalk, urodaeum and the coprodaeum merge to form the coprodaeum-urodaeum cavity. Posteriorly the coprodaeum-urodaeum cavity becomes reduced, exposing more luminal folds.

Ureters

At the level of Figure 13 the ureters exhibit positions lateral to the more or less medially located urodaeal fold which is now branched. The luminal epithelium of the ureters (Figure 15) is now taller and shows more secretory activity than in the anterior sections in Region 1. The ureters open through the urinary papillae into the coprodaeum-urodaeum cavity at this level (Figure 16)

3.1.2.3. Region 3

This region includes only the proctodaeum (see Figure 2)

At the level of Figure 17 the lumen of the coprodaeum-urodaeum cloacal cavity has become reduced to give rise to a sphincter-like structure. This indicates the start of the proctodaeum. The anterior proctodaeum has a columnar pseudostratified epithelium with columnar mucous secreting cells. At this point a fairly thick inner muscularis is evident external to the lamina propria of the proctodaeum, which is thicker ventrally than dorsally. This inner muscularis becomes reduced posteriorly. Some longitudinal smooth muscle fibre groups of the outer muscularis occur in the ventral wall of the proctodaeum. Also evident on this section is a blood plexus lateral on each side of the proctodaeum and the ventro-medially located hypoischium. Dorso-lateral in the proctodaeum wall are the dorsal glands. These glands contain columnar epithelia and are tubular,

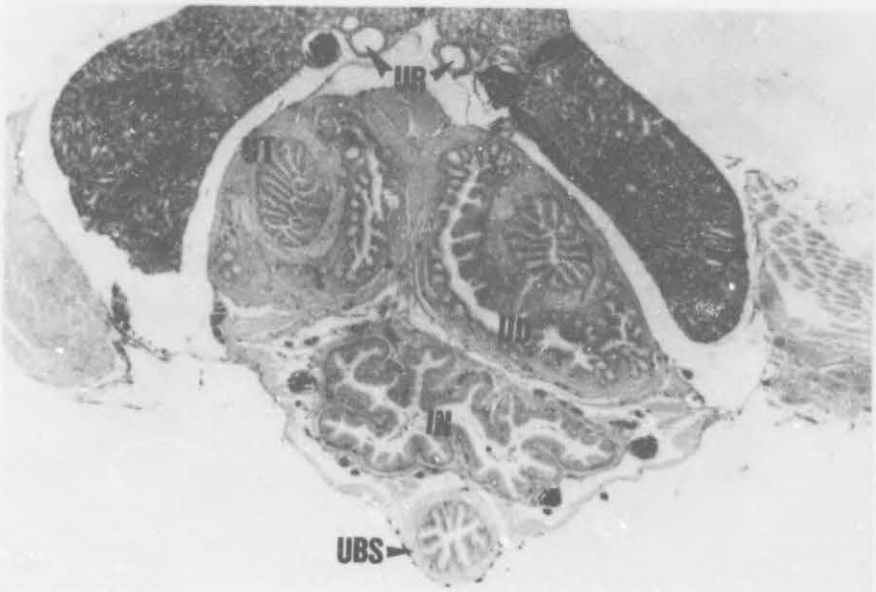

Figure 3. Section through the terminal part of the intestine (IN). Note the positions of the metanephros (MN), ureters (UR), uteri (UT), urinary bladder stalk (UBS) and the two anterior cavities of the urodaeum (UD).

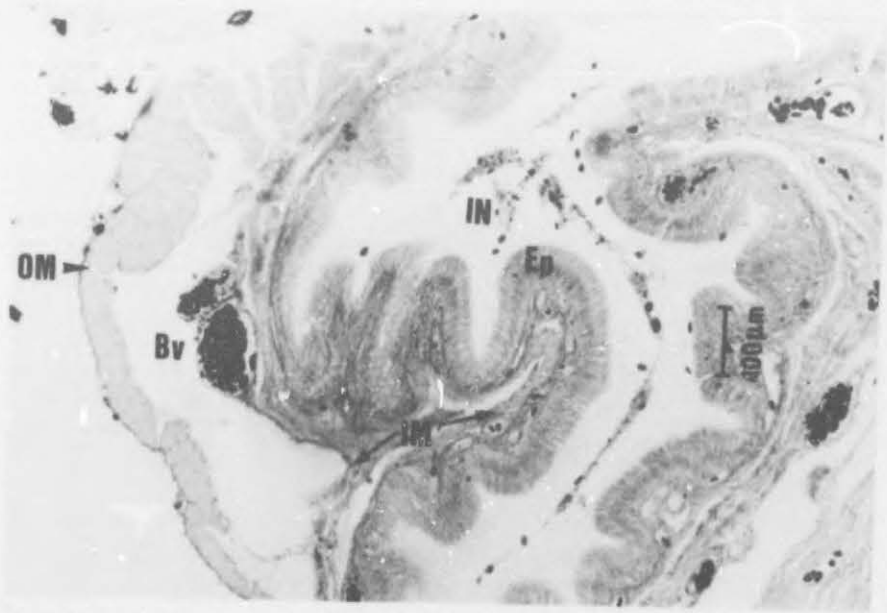

Figure 4. Higher power view (x10) showing the consisting layers of the terminal intestine. Bv=blood vessels; CT=connective tissue; Ep=epithelium; IM=inner muscularis; IN-LU=intestinum-lumen; OM=outer muscularis.

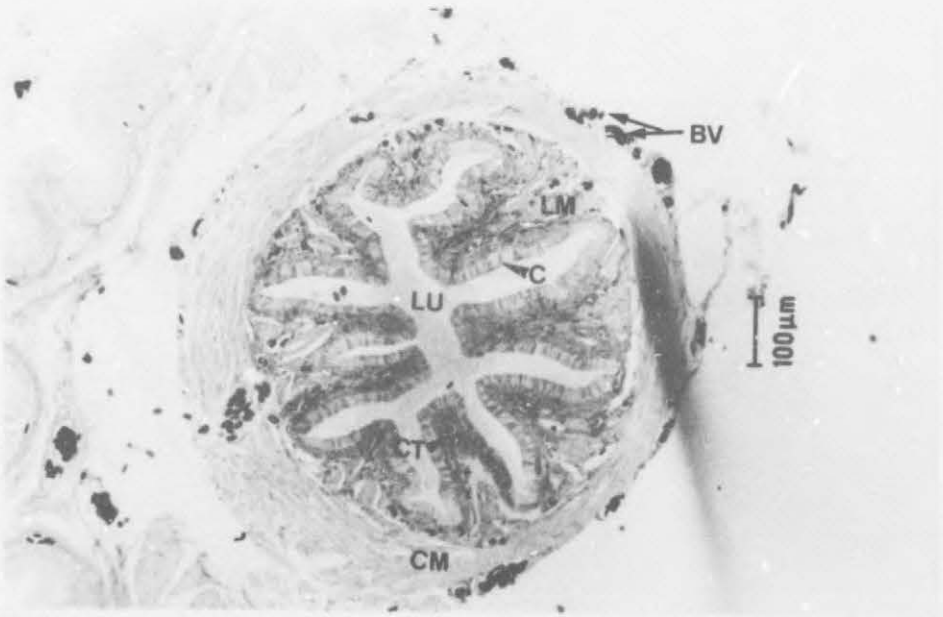

Figure 5. Higher power view (x10) of the anterior part of the urinary bladder stalk to show its consisting layers. BV=blood vessels; C =ciliated cells; CT=connective tissue; LM=longitudinal muscle fibre groups; CM=circular muscle fibres; LU=lumen.

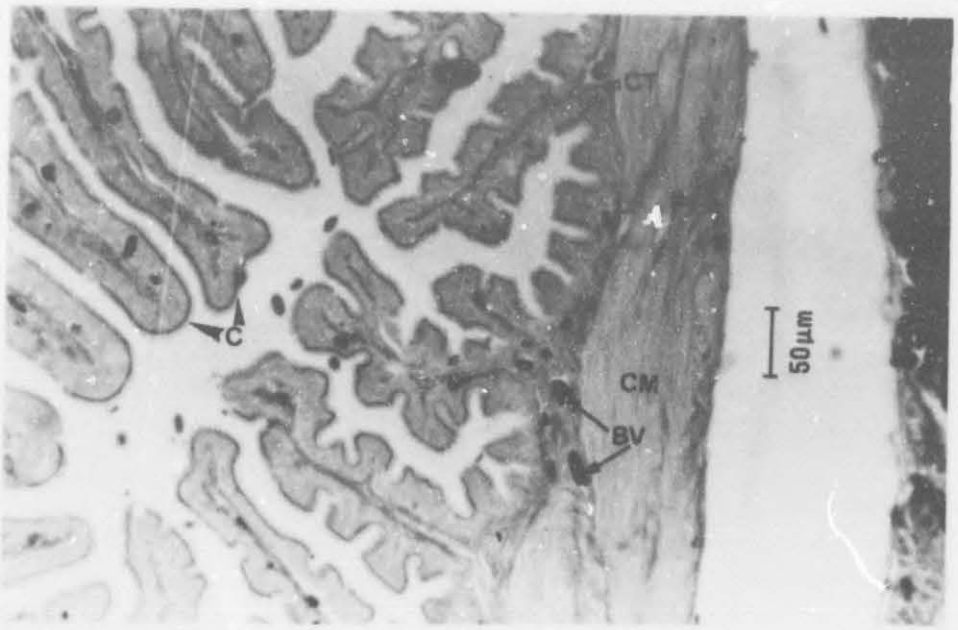

Figure 6. High power view (x20) of the anterior uteri showing its consisting layers. C=cilia, CM=circularly arranged muscle fibres; CT=connective tissue; BV=blood vessels.

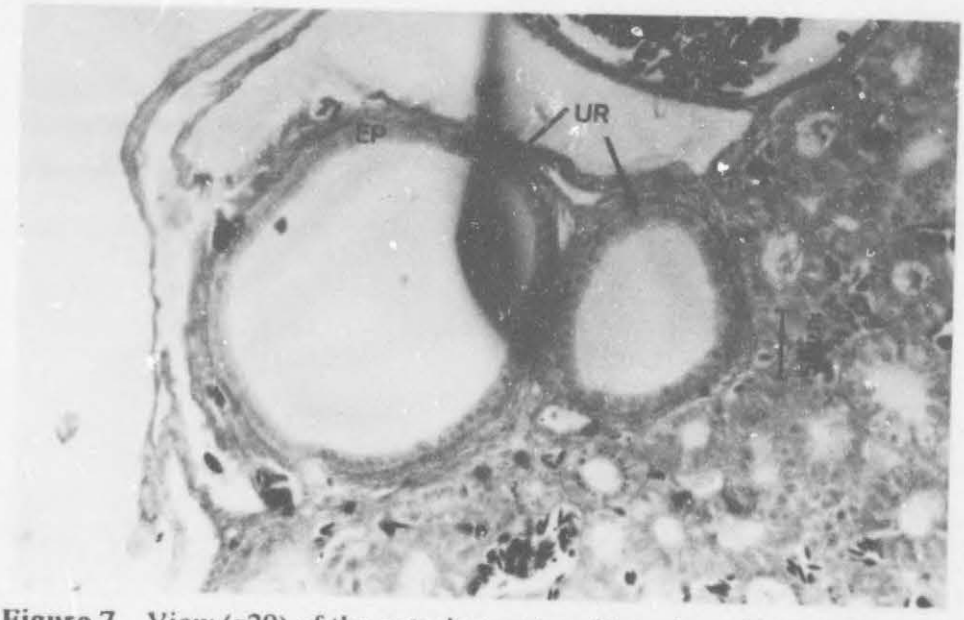

Figure 7. View (x20) of the anterior ureters. Note the cubical to columnar epithelial cells, only slightly secretory.

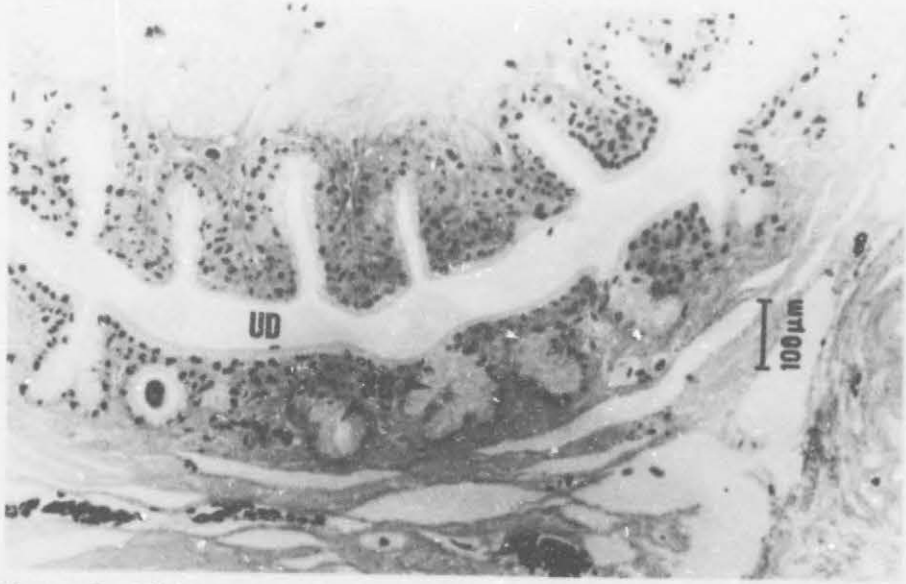

Figure 8. High power view (x10) showing the luminal epithelium of the urodaeam (UD) and that of the urodaeal glands (UG). Note the mucous secreting epithelial cells (MS) of the urodaeal glands and of the apical cells of the urodaeal epithelium..

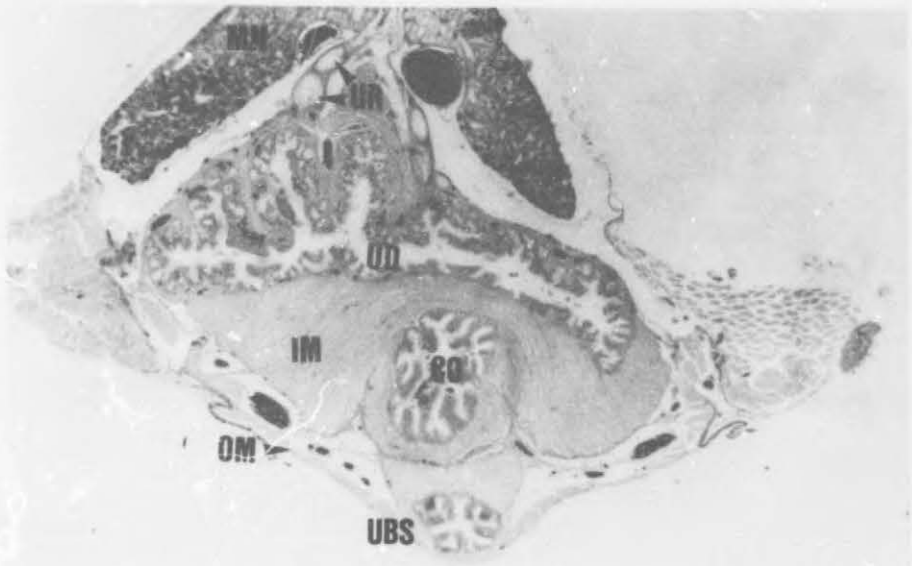

Figure 9. Section through the beginning of the coprodaeum (CO) and the common cavity of the urodaeum (UD). Note the common wall between the coprodaeaum and the urinary bladder stalk. IM=inner muscularis; MN=metanephros; OM=outer muscularis; UBS=urinary bladder stalk; UR=ureter.

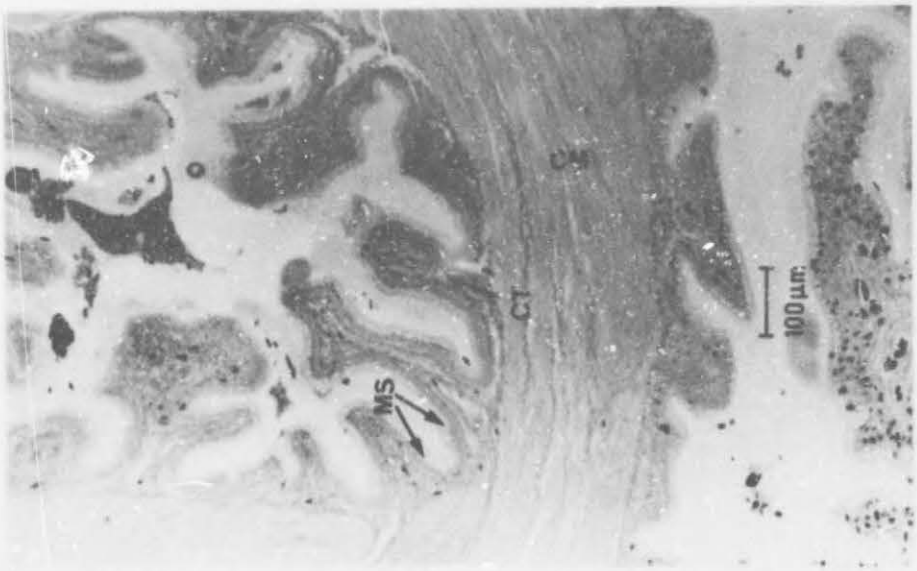

Figure 10. High power view (x10) to show the underlying layers of the coprodaeum epithelium. Note the columnar mucous secreting cells (MS) in the epithelium; CT=connective tissue; CM=circularly arranged smooth muscle fibres (CM).

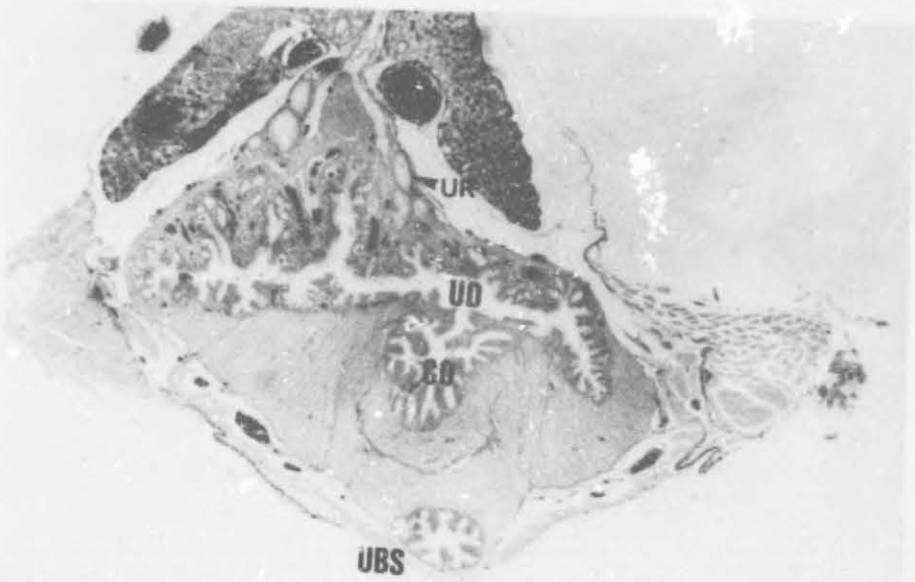

Figure 11. Section through the coprodaeum and urodaeum to show the junction between the two cloacal divisions. Note the well developed inner muscularis (IM) and the positions of the ureters (UR). BV=blood vessels.

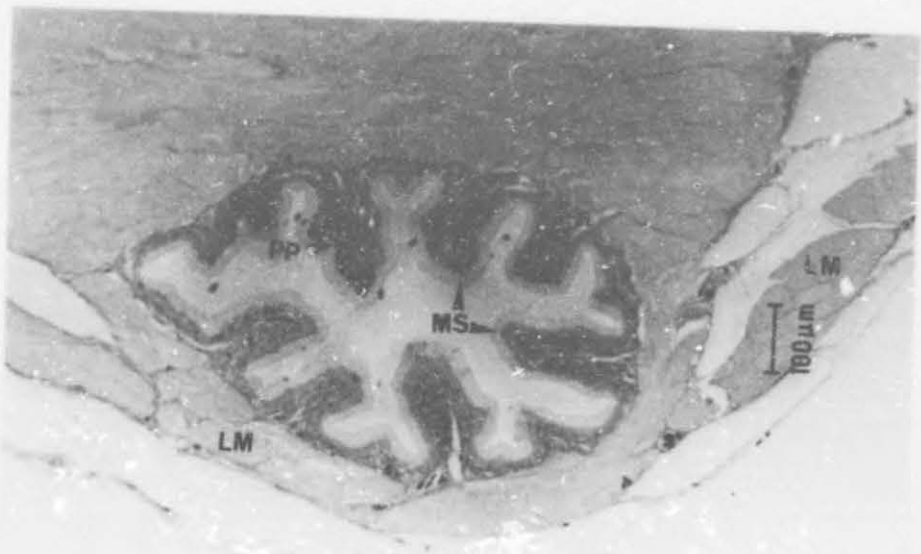

Figure 12. View (x10) of the urinary bladder stalk near its junction with the cloaca. Note the non-ciliated mucous secreting cells (MS) in the epithelium, LM=longitudinal groups of muscle fibres (LM); PP=protozoan parasites.

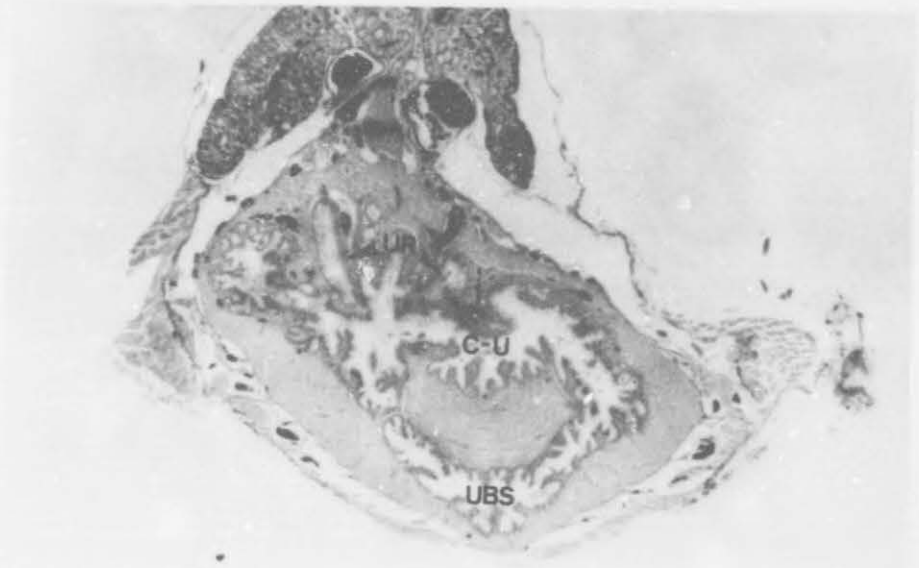

Figure 13. Section to show the junction between the urinary bladder stalk (UBS) and the coprodaeum-urodaeum (C-U). Note the positions of the ureters (UR) at this level.

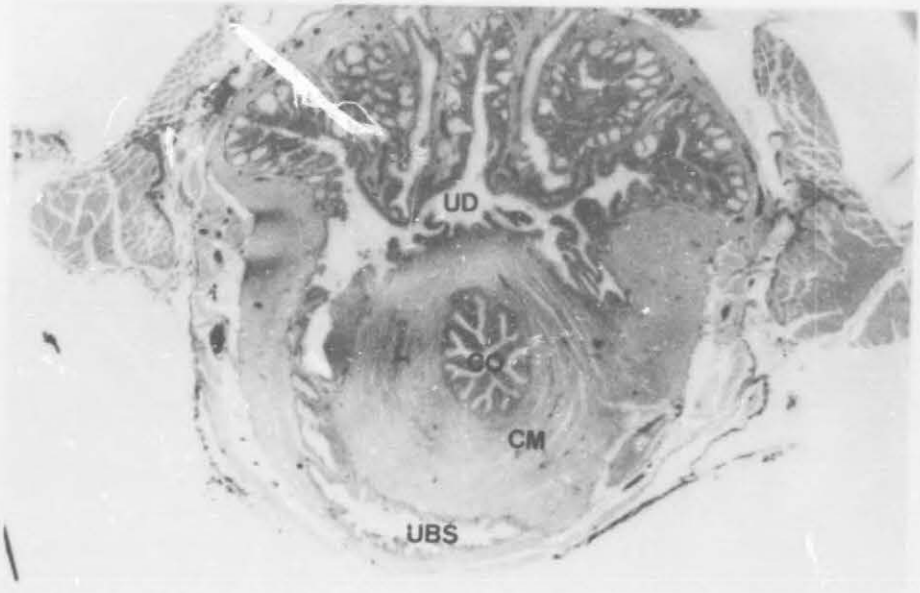

Figure 14. Low power view showing the urinary bladder stalk (UBS) junction with the urodaeum (UD) anterior to the junction between the coprodaeum and the urodaeum. Note the well developed circular arranged muscle fibre layer (CM) of the inner muscularis. CO=coprodaeum.

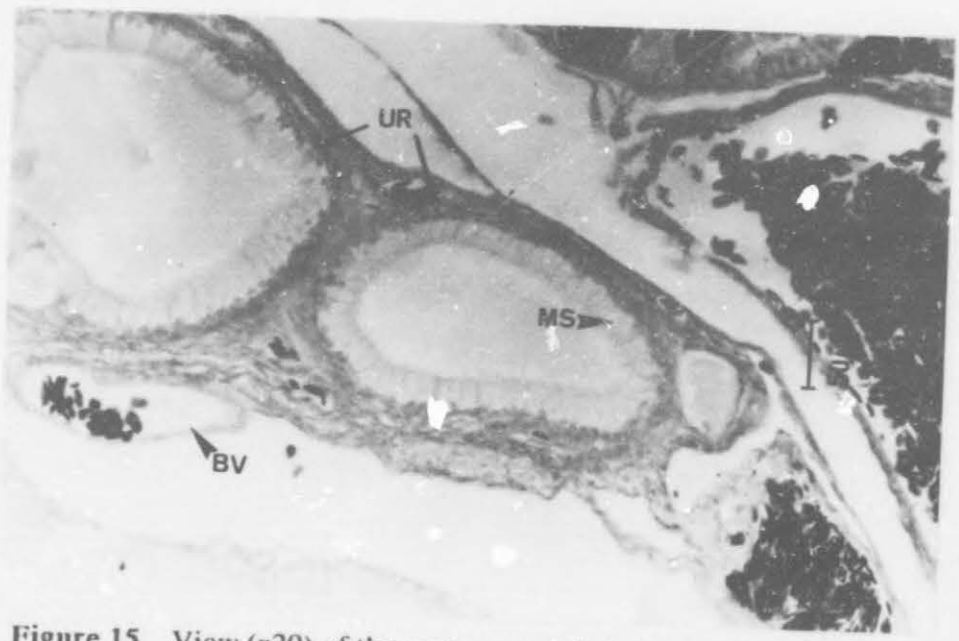

Figure 15. View (x20) of the ureters near their junctions with the vasa deferentia. Note the columnar mucous secreting cells (MS) in the ureter epithelia.

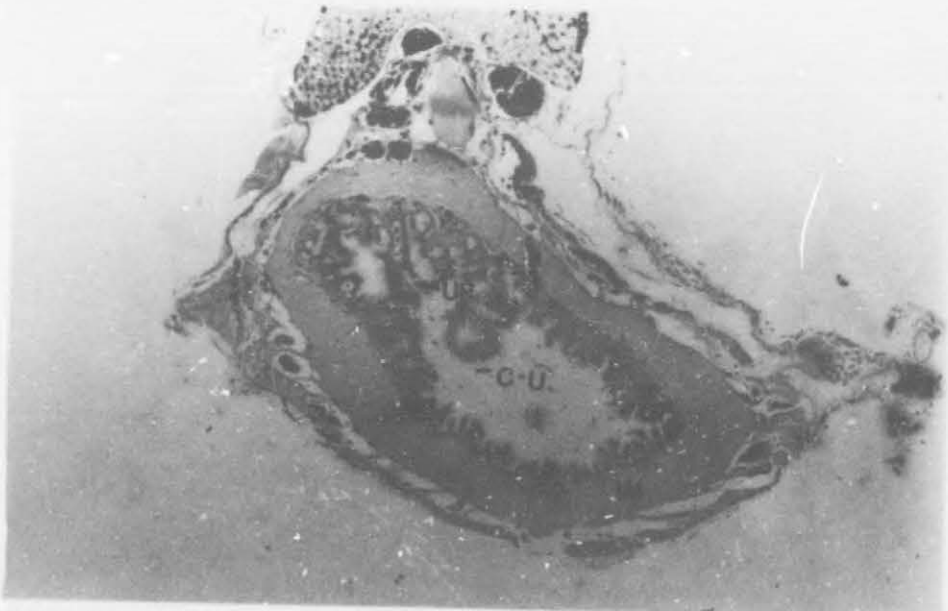

Figure 16. Section to show the junction between the right ureter and the coprodaeum-urodaeum cavity (C-U). Note the much folded luminal lining of the coprodaeum-urodaeum cavity.

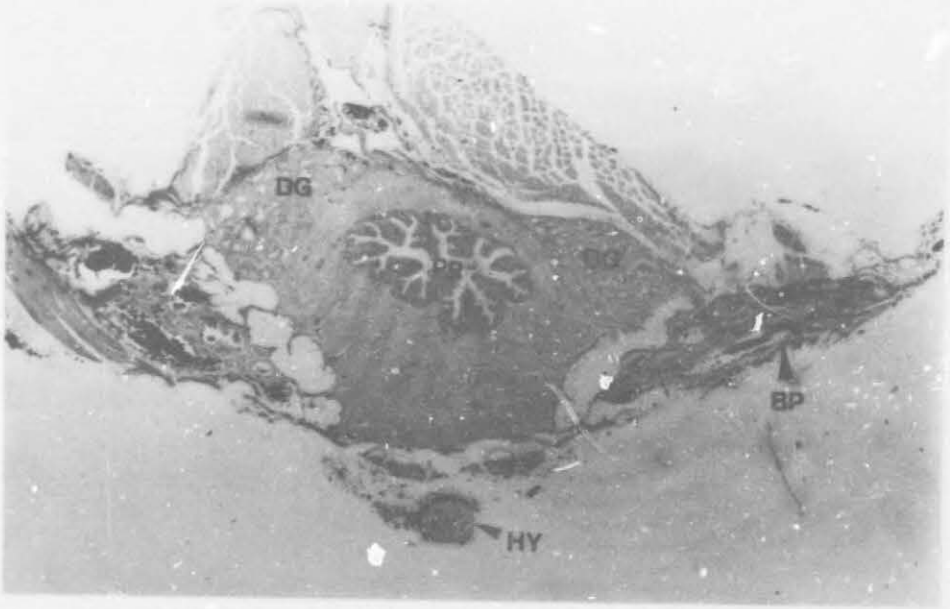

Figure 17. Section through the start of the proctodaeum. Note the dorso-laterally located dorsal glands (DG) on each side. BP=blood plexus; HY=hypoischium.

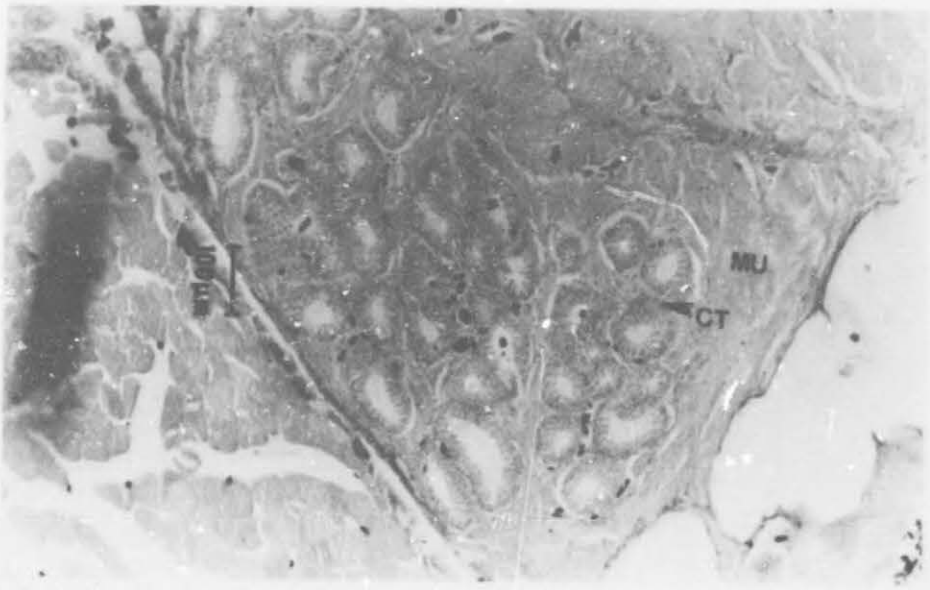

Figure 18. View (x10) of the dorsal glands. Note the columnar secreting cells in the epithelia of the gland tubule. MU=muscle fibres and connective tissue (CT).

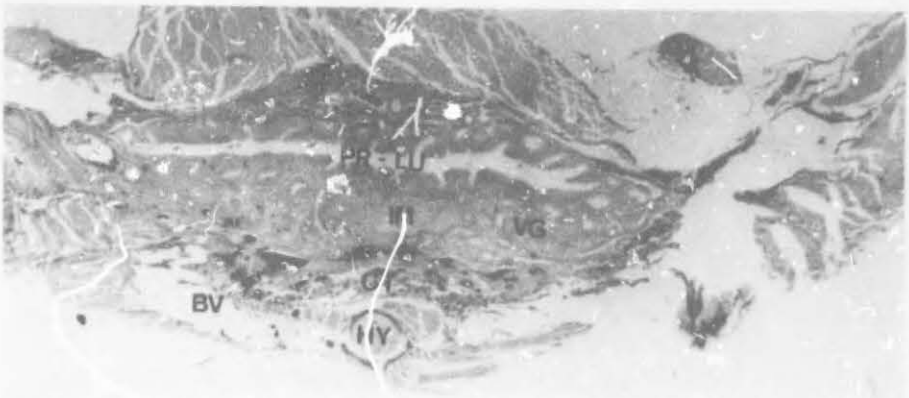

Figure 19. Section through the posterior part of the proctodaeum showing the flattened proctodaeal lumen (LU). VG=ventral glands (Vg). Note the absence of the dorsal inner muscularis. BV=blood vessels; CT=connective tissue; HY=hypoischium.

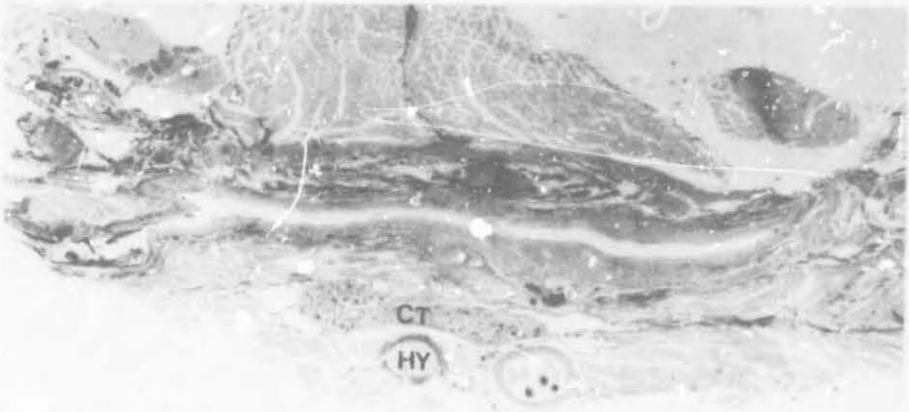

Figure 20. Section through the proctodaeum near the vent. Note the thick ventral connective tissue (CT) and the lack of dorsal glands.

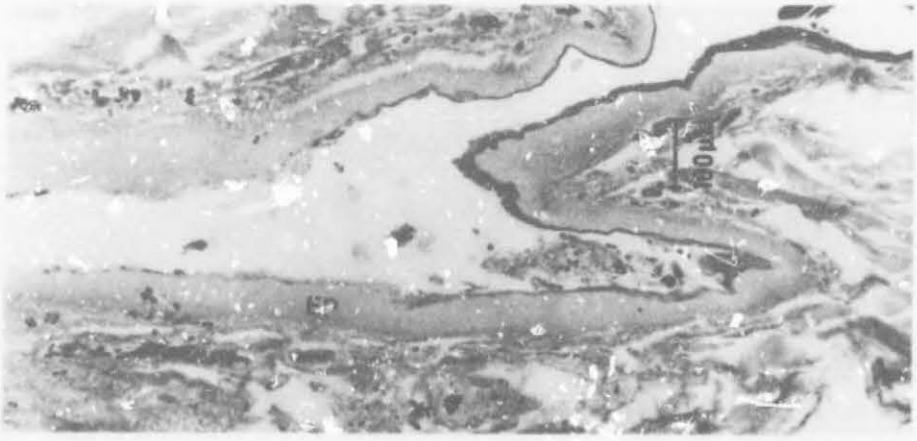

Figure 21. Higher magnification (x10) of the epithelium of the proctodaeum near the vent. A stratified, cornified epithelium (EP).

branched and exocrine. These glands contain mucous cells, but in some areas it seems as if serous cells are present among the mucous cells in the epithelium (Figure 18). Posteriorly, a group of glands (ventral glands) are visible on each side, ventro-lateral to the now flattened proctodaeum lumen (Figure 19). These glands (dorsal and ventral) also extend medially to the flattened proctodaeum. Both the dorsal and ventral glands are paired structures. The blood vessels at this point are more concentrated on the ventral and lateral sides of the proctodaeum. Only a few dorsal glands are visible in the dorsal wall of the proctodaeum, while groups of ventral glands are still evident in the ventro-lateral walls of the proctodaeum. The dorsal inner muscularis is lacking at this point, while it can still be seen in the ventral proctodaeal wall. Posterior to Figure 19 (Figure 20), the inner muscularis and the dorsal glands are lacking, while a few ventral glands are still present. The epithelium of the proctodaeum lumen changes to a cornified stratified squamous epithelium (Figure 21).

3.2. MALE

3.2.1. Gross anatomy (see Figure 22)

The male cloacal complex is more or less similar to that of the female. However, the urodaeum of the male does not exhibit anterior urodaeal limbs. Furthermore, the ureters and vasa deferentia open into the posterior extention of the urodaeum through a common urogenital opening.

3.2.2. Microanatomy

As was done for the female, the cloacal complex of the male is for reference purposes, divided into three regions (see Figure 22). Transverse sections of the cloacal complex of a male *P.melanotus* (JEM 2438, collected during spring, reproductive condition: peak of spermiogesis) from anterior to posterior, including also other male specimens, are shown in Figures 23 to 41.

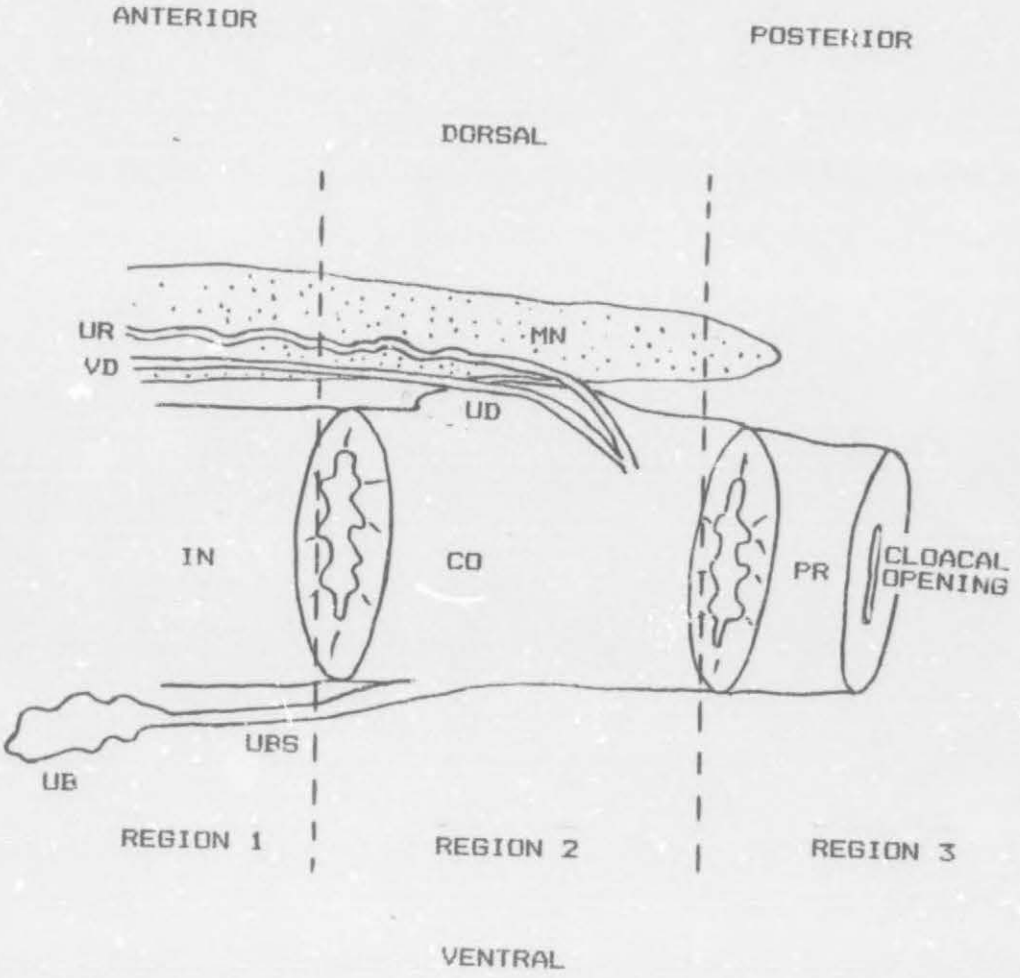

Figure 22. Diagrammatic representation of the cloacal complex of a male *P. melanotus*.
CO=coprodaeum; IN=intestine; MN= metanephros; UB=urinary bladder; UBS=urinary bladder stalk; UD=urodaeum; UR=ureter; PR=proctodaeum; VD=vas deferens.

3.2.2.1. **Region 1** (see Figure 22)

This region includes the terminal portion of the intestine, the urogenital ducts (vasa deferentia and ureters), the urinary bladder stalk and the urinary bladder. Due to the absence of urodaeal limbs in females no part of the urodaeum can be seen in this region.

Intestine

Anterior to the cloaca (Figure 23) the intestine exposes some extensive luminal folds. The epithelium of the intestine consists of columnar and goblet cells and shows seasonal variation in height (see section on seasonal variation). As described for the female (see Figure 4) a connective tissue layer (lamina propria) underlies the intestine epithelium, with an inner and outer muscularis external to it. The composition and orientation of the muscle fibres in the muscularis layers is comparable to that of the female (see Figure 4). Dorso-medial to the intestine some longitudinal smooth muscle bundles are concentrated in a prominent group.

Urinary bladder stalk

Anterior part - As in females the wall of the urinary bladder stalk consists of the three layers, the mucosa, the muscularis and the serosa, as described for the female (see Figure 5). As in females a prominent group of longitudinal muscle fibres are evident in a ventro-medial position in the lamina propria with smaller groups of longitudinal muscle fibres in a dorso-medial position and no longitudinal muscle groups evident in the lateral areas. Posteriorly, these longitudinal muscle groups become reduced (where the coprodaeum begins).

Urogenital ducts (Figure 24)

At this level (Figure 23), the vasa deferentia are located dorso-lateral to the intestine with the ureters dorso-medial to the vasa deferentia. The enlarged vas deferens on each side is filled with sperm cells and secretions, which stain intensively with Azocarmyn B. Each vas deferens is lined with a low simple cubical epithelium consisting of non-secretory cells (Figure 24). A relatively thin circularly arranged muscle fibre layer surrounds the vas deferens.

The lumina of the ureters in this section are lined with columnar epithelia which are taller than that of the vasa deferentia. The apical ends of the luminal cells of the ureters contain secretory granules which stain intensively with Azocarmyn B. Such secretory granules were not observed in the ureters of the female specimens examined. Intensively staining secretions are also present in some of the ducts in the metanephros.

3.2.2.(ii). Region 2

This region includes the coprodaeum, the urodaeum, the urinary bladder stalk and the urogenital ducts. The urinary bladder stalk and the urogenital ducts join the cloaca in this region.

Coprodaeum

At the level where the coprodaeum is discernable, posteriorly pointing blind-ending cavities of the intestine, can still be seen (Figure 25). In contrast to the columnar pseudostratified epithelium of the intestine which consists of columnar and goblet cells, the pseudostratified epithelium of the coprodaeum consists of mucous secreting cells (Figure 26). The coprodaeum possesses the same underlying layers as described for the female (see Figure 12). Underlying the coprodaeum epithelium is a layer of connective tissue (lamina propria) followed by a well developed inner muscularis and an outer muscularis. The inner

muscularis is more developed than the inner muscularis of the terminal intestine and is primarily composed of circularly arranged smooth muscle fibres.

Urinary bladder stalk

Posterior part - The urinary bladder stalk at this level shows a more enlarged lumen, lined with unciliated mucous secreting cells (Figure 27). A common wall exists between the stalk and the coprodaeum, which is largely composed of circularly arranged smooth muscle fibres. Posteriorly (Figure 28), a passageway occurs between the coprodaeum and the stalk. The passageway begins anteriorly as a medially located vertical canal. Posteriorly the junction between the urinary bladder stalk and the coprodaeum enlarges (see Figure 30 and 32). In the three male specimens examined the junction between the urinary bladder stalk and the cloaca was anterior to the coprodaeum-urodaeum junction - either with the coprodaeum (Figure 28) or with the terminal intestine and the coprodaeum (Figure 29). In the case of junction with the terminal intestine the flattened bladder stalk is connected by means of vertical canals (Figure 29). These canals are lined by the same type of epithelium as that of the bladder stalk, namely a columnar pseudostratified one. This junction, which connects the bladder stalk with the terminal intestine extends posteriorly to connect the bladder stalk with the coprodaeum. More posteriorly, the junction between the bladder stalk and the coprodaeum enlarges.

Urodaeum

Posteriorly, the urodaeum is evident dorsal to the coprodaeum (Figure 30). Sperm cells and red staining secretions are contained in the urodaeal lumen. The lumen of the urodaeum is lined with a pseudostratified columnar epithelium consisting of apical mucous secreting cells (Figure 31). In contrast to the urodaeum of the female, no urodaeal glands are found in the urodaeal walls of the males. A common wall exists between the coprodaeum and the urodaeum,

which is thicker than the common wall between the latter divisions in the female. Posteriorly, a passageway is formed between the urodaeum and the coprodaeum (Figure 32). In this specimen this junction (anteriorly) between the urodaeum and coprodaeum is in a lateral position, with a much enlarged junction between the lumen of the urinary bladder stalk and the coprodaeum at this level. Posteriorly, the inner muscularis between the urodaeum and coprodaeum disappears from view, resulting in a much enlarged coprodaeum-urodaeum cavity (Figure 33).

At the level of Figure 35 some ventral and lateral folds extend into the coprodaeum-urodaeum cavity. Ganglion cells and a blood plexus occur laterally on each side of the coprodaeum-urodaeum inner muscularis. On the one lateral side (and posteriorly on both sides) group of ganglion cells are evident on the inside of the blood plexus.

Urogenital ducts

At the level of Figure 33 each ureter occupies a lateral position on the inside of each vas deferens, of which the lumina are now reduced. The muscle layer which surrounds the vas deferens is now thicker (Figure 34). Anterior to the junction with the coprodaeum-urodaeum cavity the lumen of the ureter becomes more flattened and extends ventrally to the vas deferens (see Figure 33). In contrast to the situation found in the female where the urogenital ducts (uteri and ureters) empty separately into the cloaca, the ureter and vas deferens of males coalesce before opening into the coprodaeum-urodaeum cavity (Figure 35). The urogenital openings in the cloaca of the male are in more or less the same position as the openings of the ureters in the coprodaeum-urodaeum cavity in females.

4.2.3. Region 3

This region only includes the proctodaeum.

The proctodaeum begins as a sphincter-like structure, which dorsally is still in connection with the posteriorly extended coprodaeum-urodaeum cavities (Figure 36). Located in a lateral position on each side of the proctodaeum is a blood plexus and a smooth muscle bundle which is infiltrated by an enlarged blood vessel.

In contrast to the situation in the female, the ventral glands are evident anterior to the dorsal glands. As in females, these ventral glands are tubular, branched and exocrine but they are more branched and more prominent in males. These glands are lined with columnar epithelial cells (Figure 37). Posteriorly (Figure 38), dorsal glands occur dorso-laterally in the proctodaeum wall. More posteriorly, these glands (dorsal and ventral) also extend to a more medial position. The dorsal glands are of the same type as the ventral glands. The proctodaeum is lined by secretory and non-secretory cells. Dorso-lateral to the proctodaeum paired ganglia can be seen in close association with enlarged blood vessels. In a position ventro-medial to the proctodaeum the hypoischium can be identified. External and ventral to the ventral glands is a relatively thick connective tissue layer infiltrated by blood vessels and 'blood migrant cells'.

Posteriorly (Figure 39), the proctodaeum lumen becomes flattened and exposes lateral evaginations. The ventral inner muscularis is lacking at this point while the dorsal and ventral glands dominate the proctodaeum wall. These dorsal and ventral glands open into the proctodaeum by means of a few ducts. Near the vent the inner muscularis and the ventral glands are lacking in the proctodaeum wall, while some dorsal glands can still be seen (Figure 40). The opposite was found in the females where the dorsal glands were lacking near the vent, while some ventral glands were still evident. The epithelium of the proctodaeum changes to a cornified stratified squamous epithelium (Figure 41).

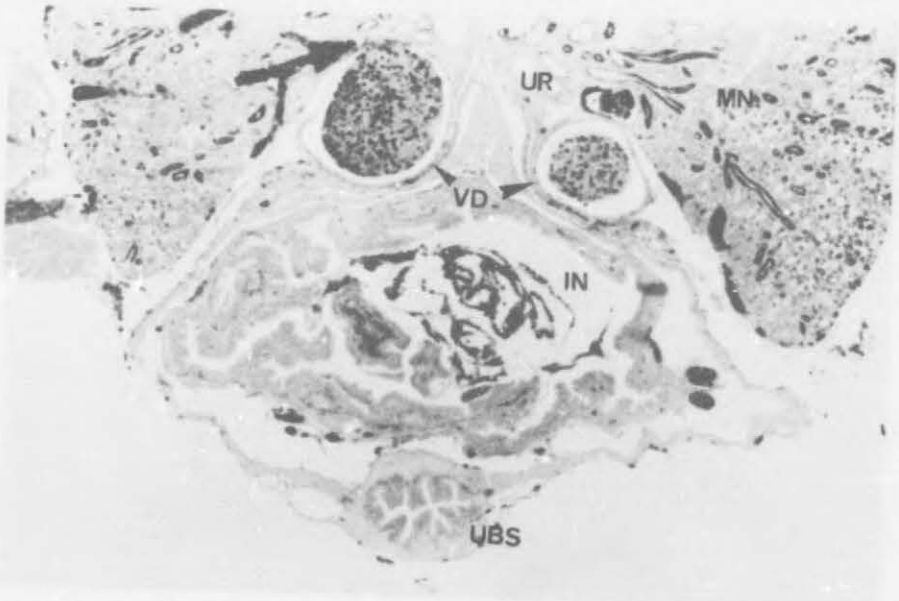

Figure 23. Section through the terminal intestine (IN). Note the position of the metanephros (MN), enlarged vas deferens (VD), ureters (UR) and the urinary bladder stalk (UBS).

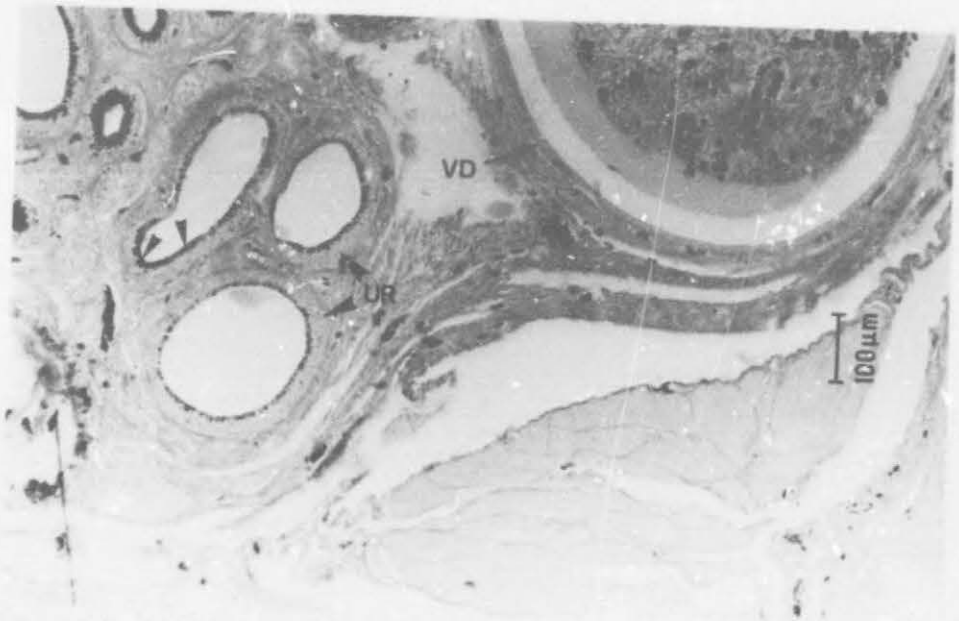

Figure 24. High power view (x10) of Figure 23 to show the epithelia of the ureters (UR) and that of the vasa deferentia (VD). Also take note of secretory granules in the epithelia of the ureters and in the vas deferens (arrows).

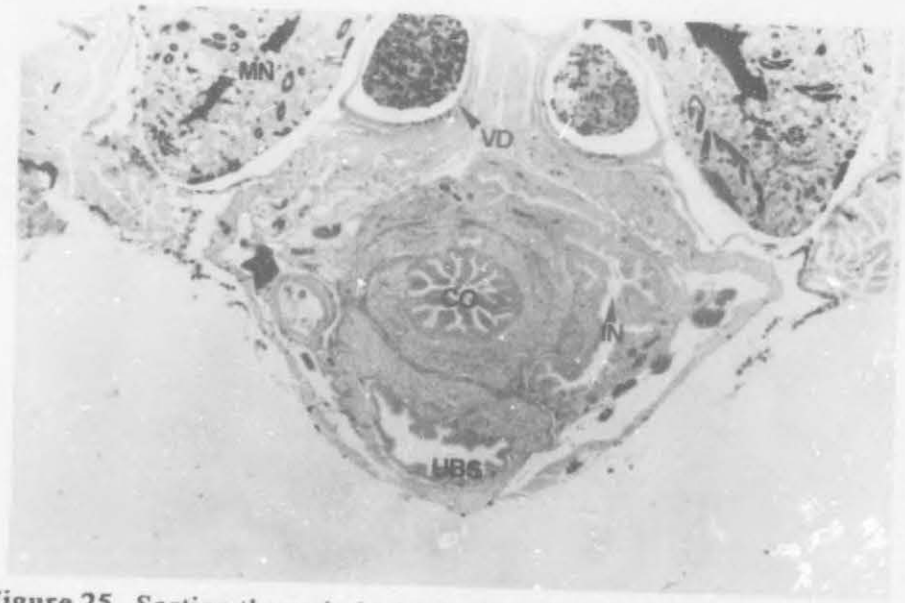

Figure 25. Section through the beginning of the coprodaeum (CO) and the posterior part of the urinary bladder stalk (UBS). Note the enlarged lumen of the urinary bladder stalk and the posterior blind ending intestinal cavities (IN).

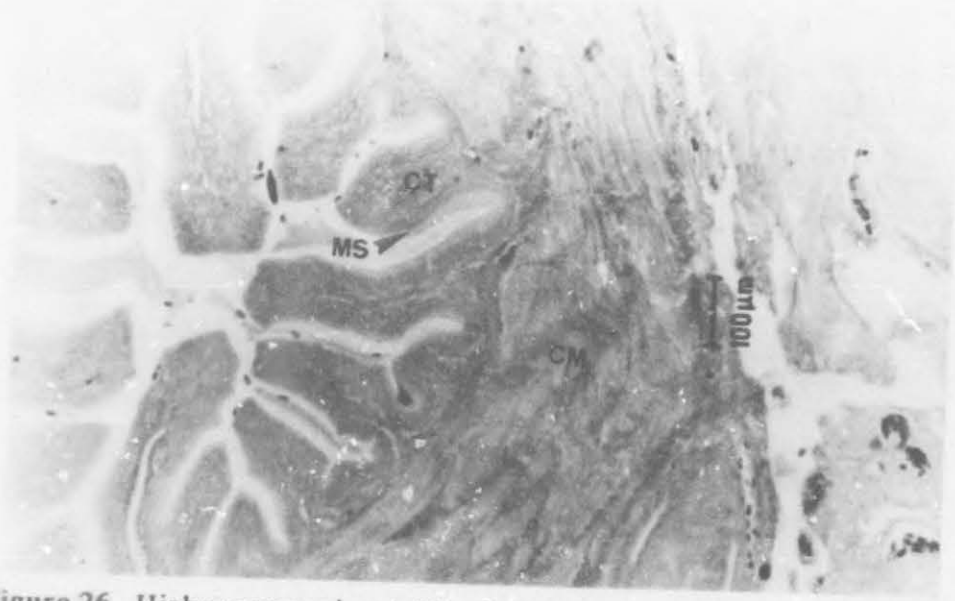

Figure 26. Higher power view (x10) of the coprodaeum to show its consisting layers. CM=circularly arrange muscle fibres; CT=connective tissue; MS=mucous secreting cells.

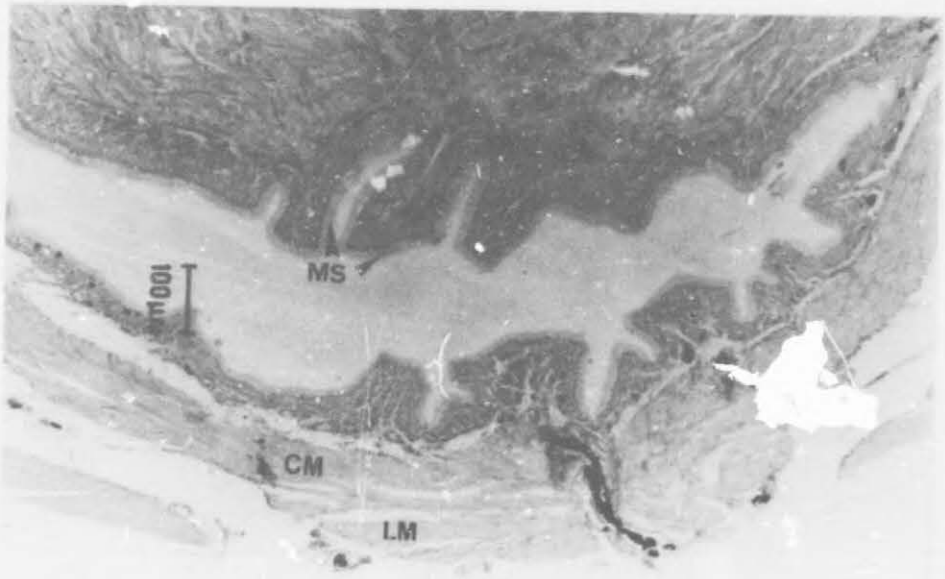

Figure 27. Higher power (x10) view of the urinary bladder stalk (UBS) near its junction with the coprodaeum. MS = mucous secreting cells; CM = circularly arranged muscle fibres; LM = longitudinal muscle fibre groups.

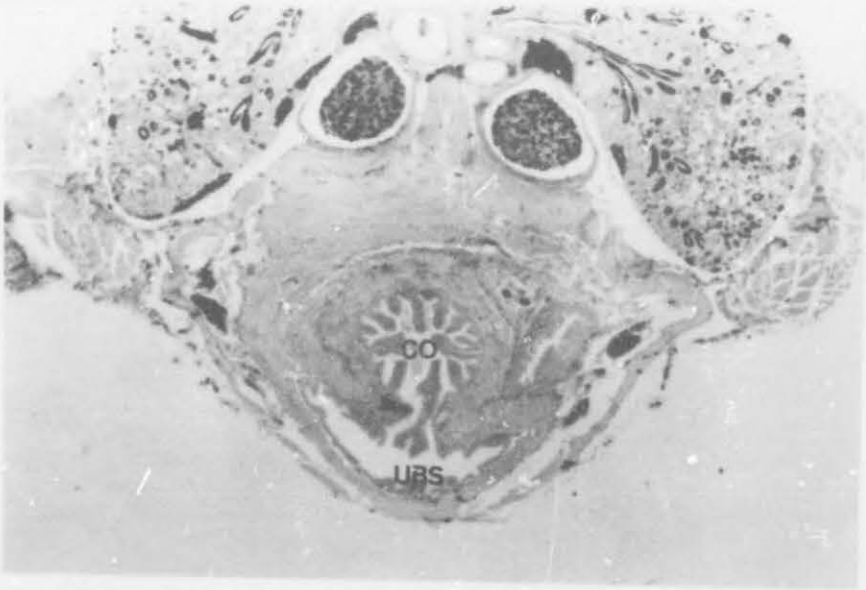

Figure 28. Section to show the junction between the urinary bladder stalk (UBS) and the coprodaeum (CO) posterior to the terminal intestine.

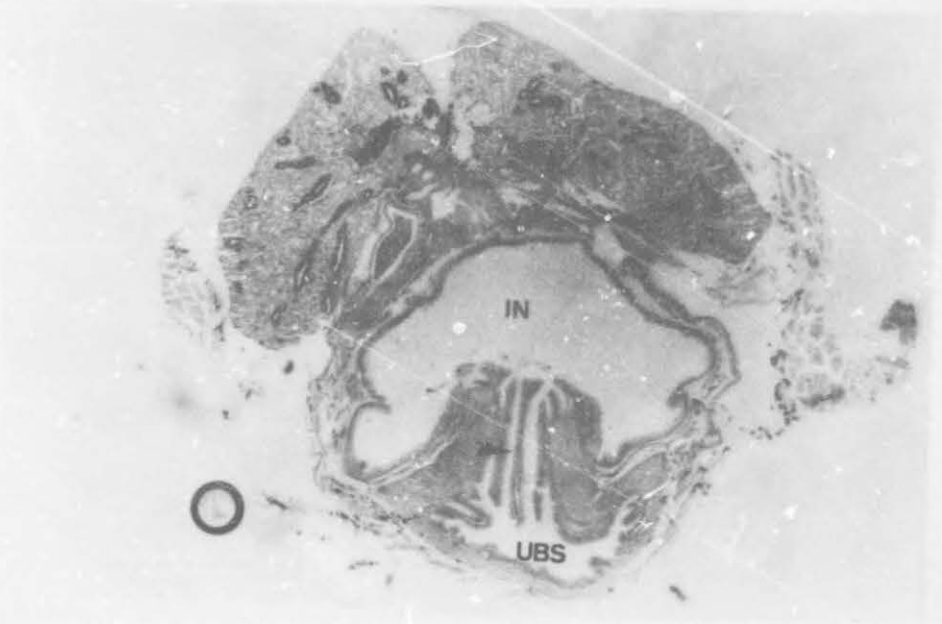

Figure 29. Section through the terminal part of the intestine, where the coprodaeum starts, to show the junction of the urinary bladder stalk (IN) with the intestine (IN).

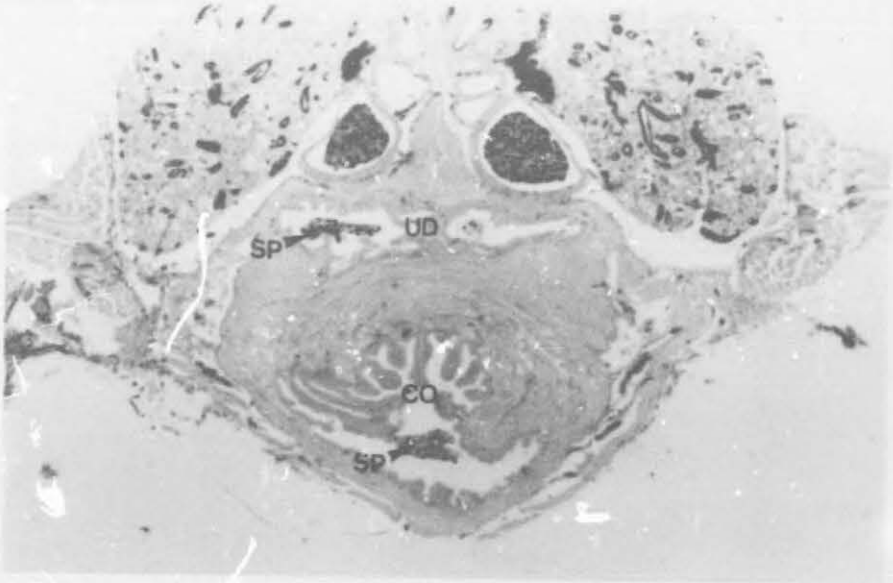

Figure 30. Section through the urodaeum dorsal to the coprodaeum. Note the presence of sperm (SP) in the cavities of the urodaeum and in that of the coprodaeum (CO).

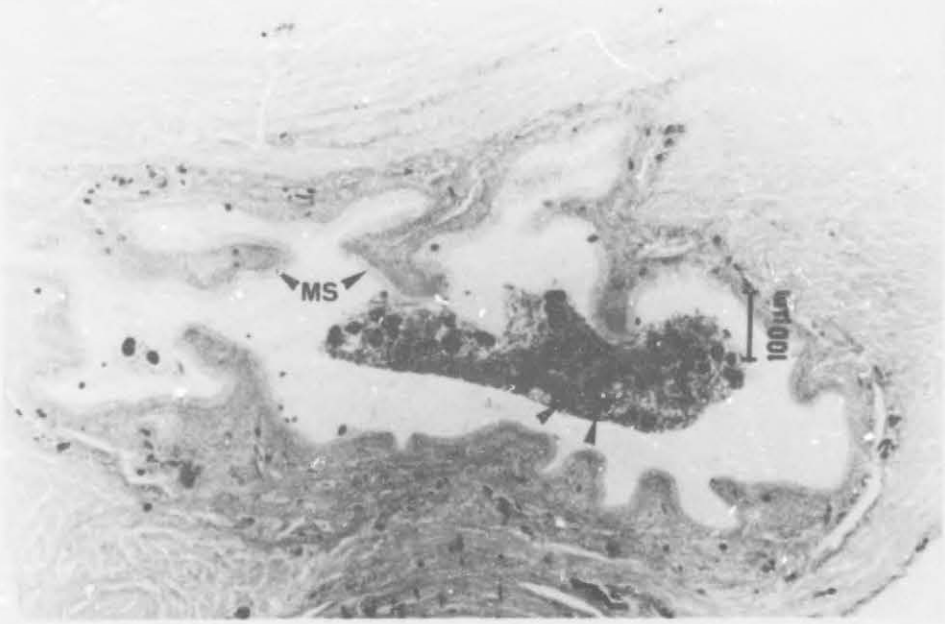

Figure 31. High power view (x10) of the urodaeum to show its luminal epithelium of the urodaeum. Note the sperm (SP) with extensive staining secretions (arrows) among them in the lumen of the urodaeum. MS = mucous secreting cells

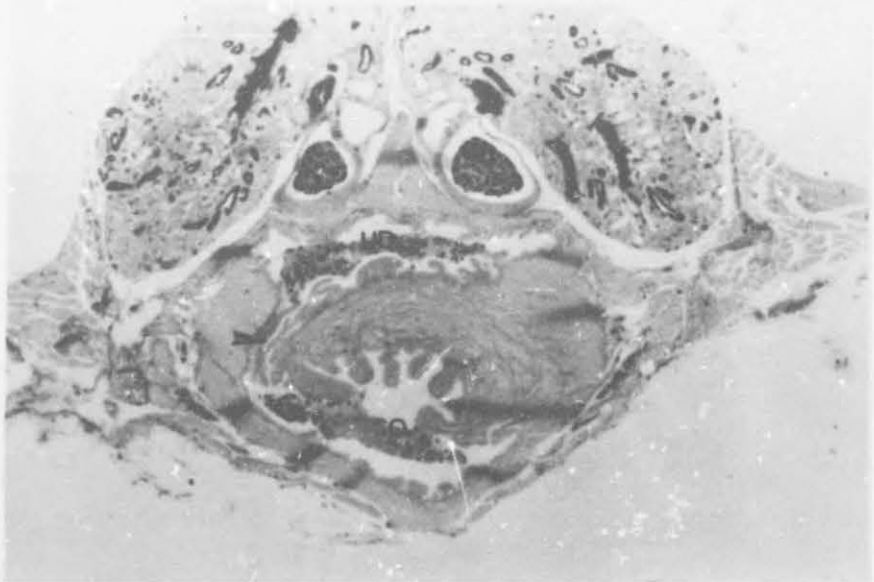

Figure 32. Section through the coprodaeum (CO) and urodaeum (UD) showing the junction between these two divisions (arrow).

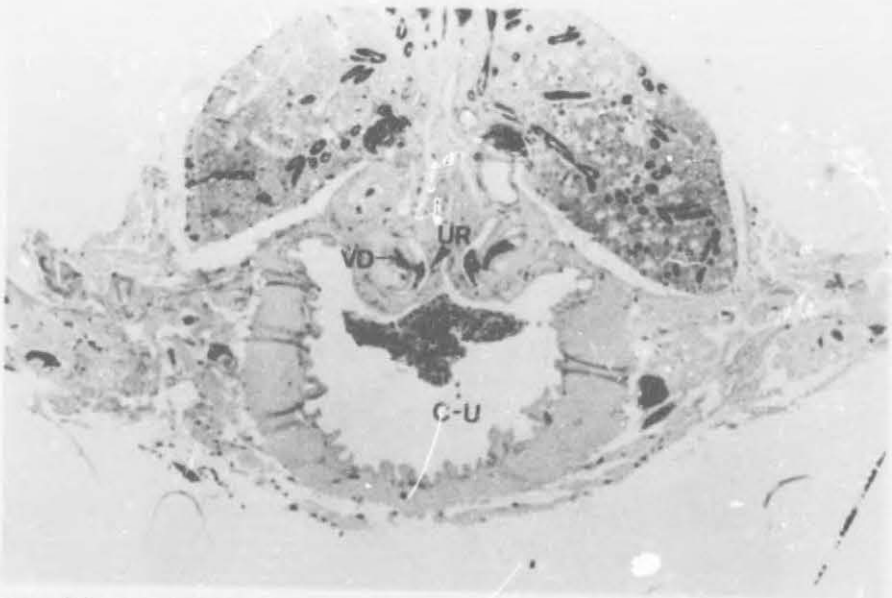

Figure 33. Section (low) through the coprodaeum-urodaeum cavity (C-U) to show the enlarged lumen (LU) and the junction of the vas deferens (VD) with the ureter (UR) on each side.

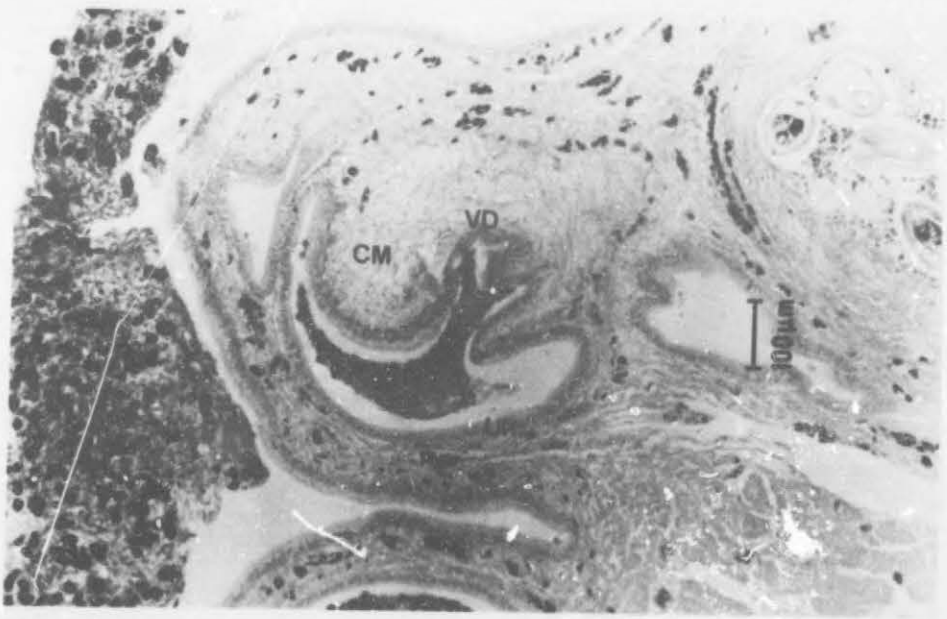

Figure 34. Higher magnification (x10) to show the junction of the vas deferens with the ureter. Note the relatively thick circularly arranged smooth muscle layers (Cm) in the vas deferens wall.

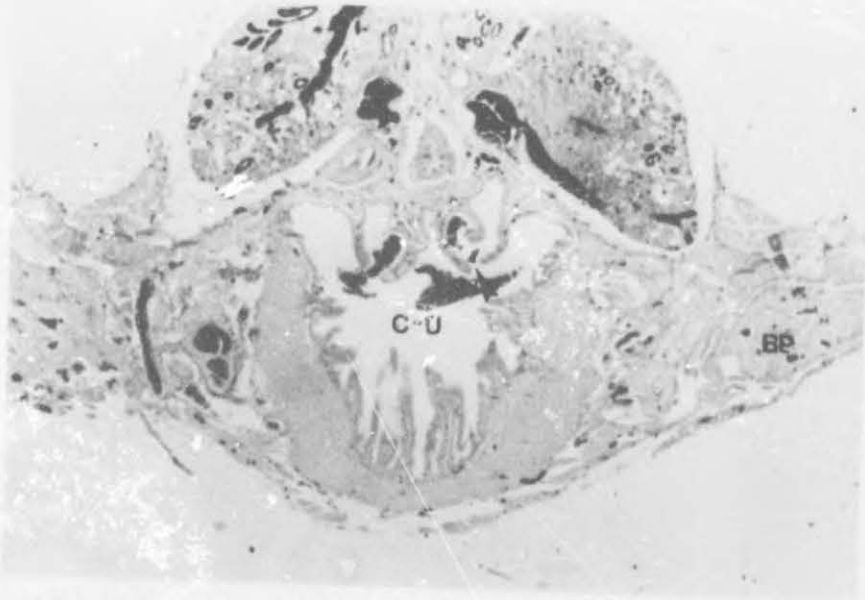

Figure 35. Section through the coprodaeum-urodaeum (C-U) cavity to show the tall luminal folds and the junction between the urogenital ducts and the cloacal cavity.

Figure 36. Section through the start of the proctodaeum (PR). Note the presence of the first group of ventral glands (VG) and the blood plexis on each side. MU = muscle fibre group

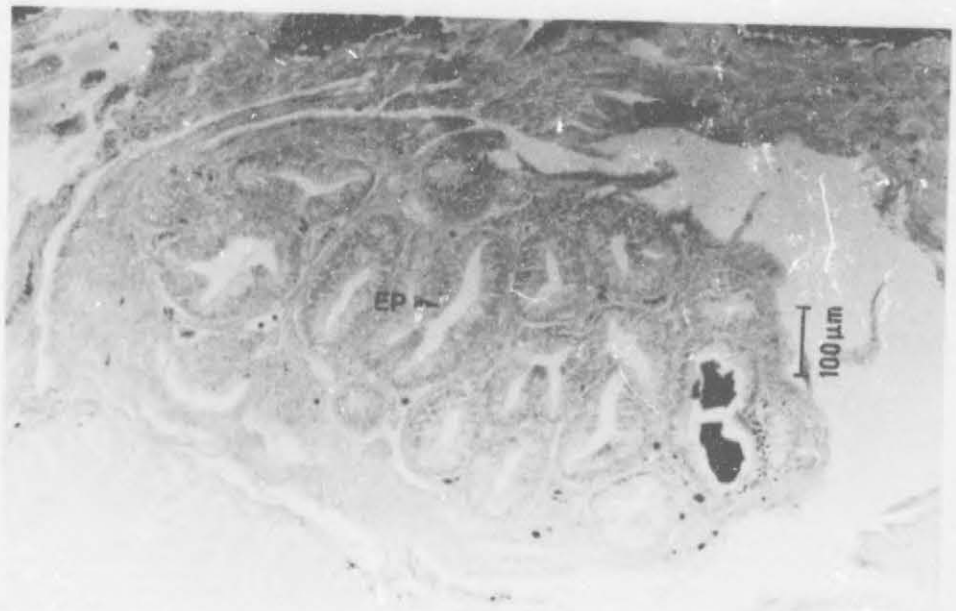

Figure 37. High power view of the ventral glands to show their columnar serous secreting epithelial cells.

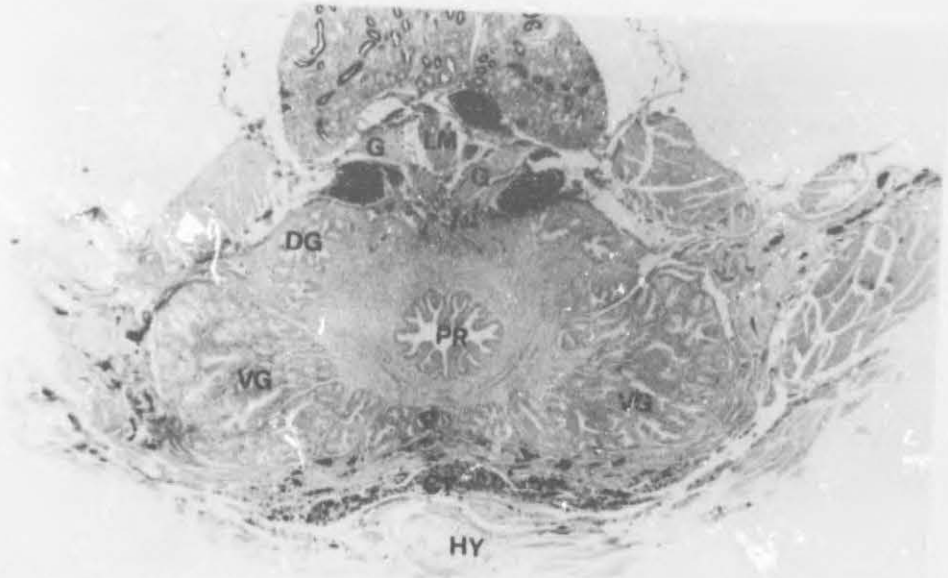

Figure 38. Section through the proctodaeum showing the dorsal- and ventral glands. G=ganglion cells; LM=prominent group of longitudinal muscle fibres; CT=connective tissue; HY=hypoischium.

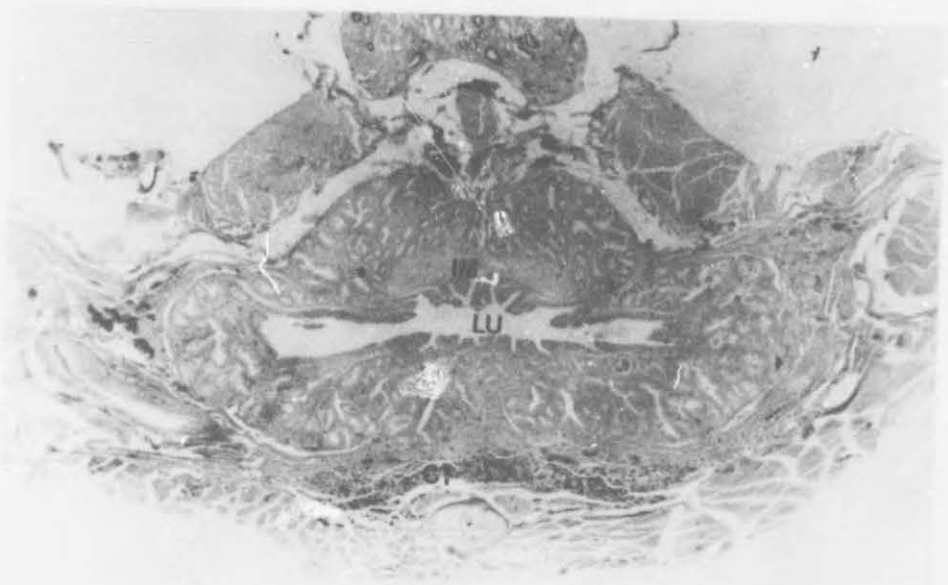

Figure 39. Section through the posterior part of the proctodaeum to show the more flattened lumen (LU). Note that only the dorsal inner muscularis (IM) is still present. CT=connective tissue; MU=bundles of muscle fibres.

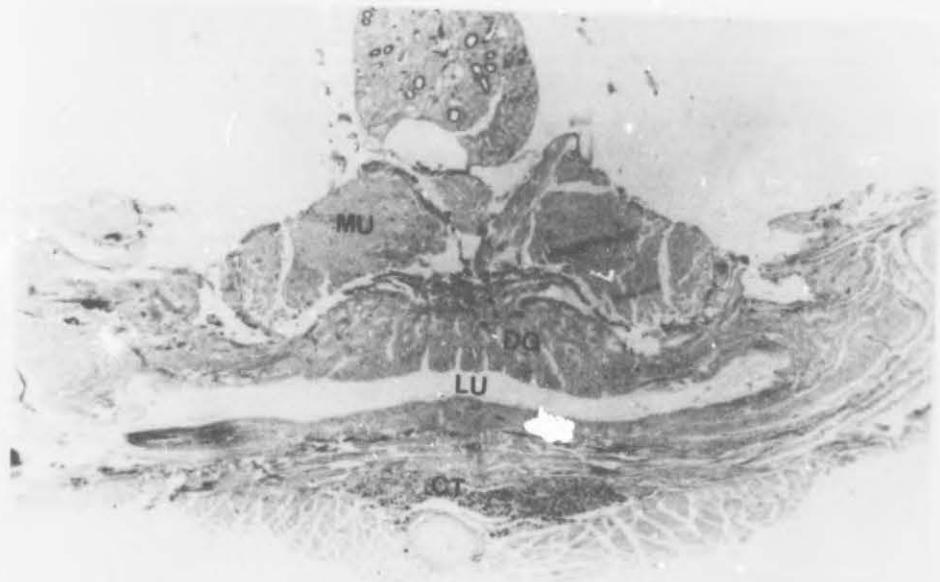

Figure 40. Section through the proctodaeum near the vent. Note that the dorsal glands empty into the proctodaeum at this level. MU=muscle fibres.

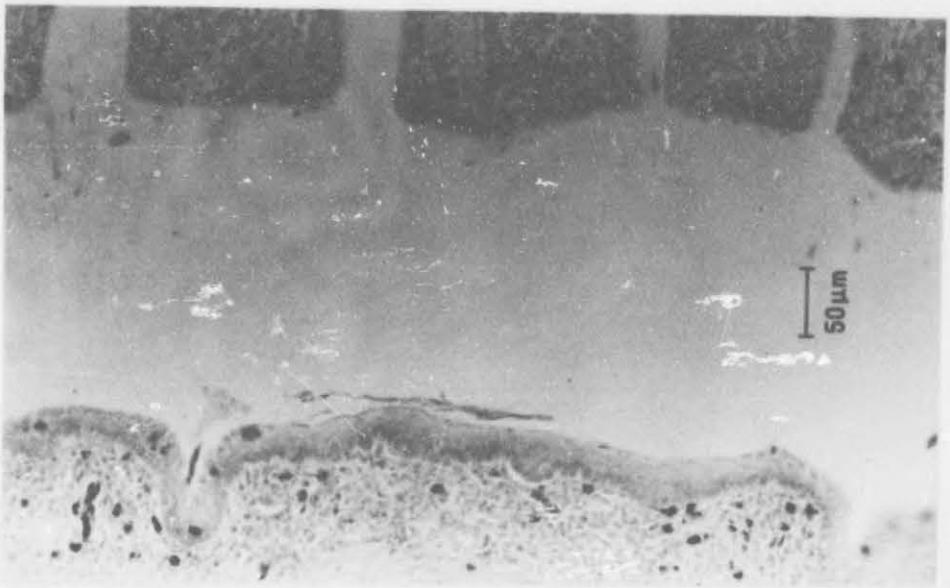

Figure 41. High power view of the proctodaeum epithelium near the vent to show the ventral stratified squamous, epithelium and the cubical cells of the dorsal epithelium.

4.3. SEASONAL VARIATION

Only a limited number of animals have been examined and observations regarding seasonal variation in cloacal microanatomy cannot be considered as conclusive. However, in the animals investigated, which were collected during and after or before the breeding season, the following variations in the anatomy of the cloacal complexes of females and males were observed:

4.3.1. Females

Intestine anterior to cloaca

The intestinal epithelium in the females examined showed variation in height. However, more animals should be investigated to establish whether this represents seasonal changes in thickness or whether it is simply the result of intraspecific variation.

Urodaeum

In non-gravid females collected after the breeding season, the epithelial lining of the urodaeum showed greater secretory activity (Figure 42) than the lining in the gravid females which was reduced (Figure 43).

No seasonal variation in secretory activity of the dorsal and ventral glands could be established in females.

4.3.2. Male

Intestine anterior to the cloaca

As was found for the gravid females, the intestinal epithelium showed variation in height. As in females more animals should be examined to determine if this is a seasonal phenomenon.

No seasonal variation in the secretory activity of the dorsal and ventral glands of the males could be established.

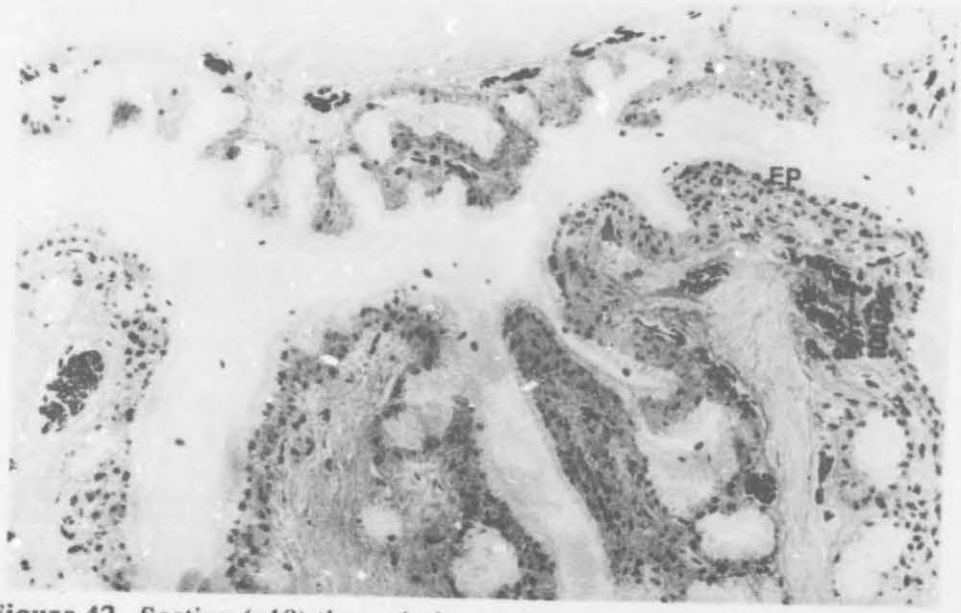

Figure 42. Section (x10) through the urodaeum to show the secretory cells of the urodaeal epithelium in a non-gravid female.

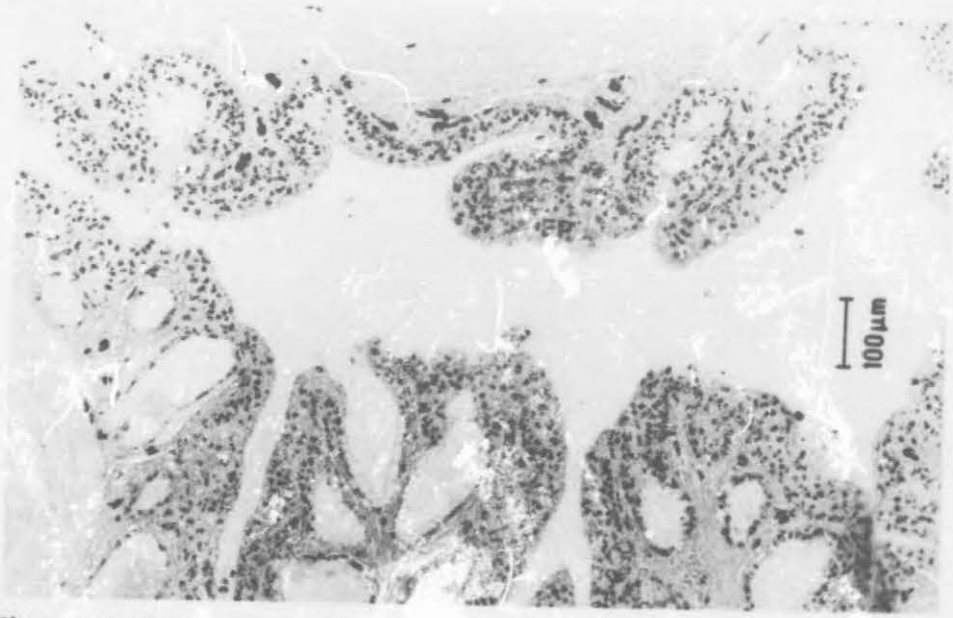

Figure 43. Section (x10) to show the non-secretory (NS) urodaeal epithelial cells in a gravid female.

CHAPTER 4

ANATOMY OF THE CLOACAL COMPLEX OF *CORDYLUS* *CORDYLUS*.

4.1. FEMALE

4.1.1. Gross anatomy

As in *P. melanotus* three divisions of the cloaca can be identified: the coprodaeum, urodaeum and proctodaeum. The urodaeum is a dorsal forward extension of the cloaca. The anterior urodaeum is divided into two urodaeal limbs, dorso-lateral on each side of the coprodaeum. The urinary bladder stalk extends ventrally from the cloaca and connects the urinary bladder with the cloaca. The uteri and the ureters run backwards between the coprodaeum and the metanephros and open separately through the dorsal wall of the cloaca; the uteri in the anterior urodaeum and the ureters in the coprodaeum-urodaeum cavity.

4.1.2. Microanatomy

For purposes of the microanatomical description, the cloacal complex was arbitrarily divided into three regions, as was done for *P.melanotus* (see Figure 2). In the description of the cloacal complex of the female of *P. melanotus*, Region 1 included the part anterior to the cloacal complex only, in other words the terminal part of the intestine, the urinary bladder, the urinary bladder stalk and the urogenital ducts (vasa deferentia and ureters). In this specimen, however, Region 1 would have included uteri which are still flattened and a urinary bladder stalk which is still in connection with the urinary bladder stalk, exposing a flattened lumen. For purposes of comparison of the above mentioned structures, with that of the female *P. melanotus* described in the previous chapter, Region 1 of this specimen will include the beginning of the coprodaeum too.

Figures 44 to 65 represent a series of transverse sections through the cloacal complex of a female *Cordylus cordylus* (JEM 165, in an advanced vitellogenic stage) from anterior to posterior, with variations as observed in other female specimens also r

4.1.2.1. **Region 1** (see Figure 2)

This region encompasses the terminal portion of the intestine, the beginning of the coprodaeum, the urogenital ducts (uteri and ureters) and the anterior part of the urinary bladder stalk. In contrast to *P. melanotus* where the urodaeal limbs extended forward to exhibit a position dorsal to the terminal intestine the urodaeal limbs are first observed posterior to where the coprodaeum begins (in Region 2).

Dorso-lateral to the coprodaeum are the uteri and dorso-medial to the latter are the ureters. Prominent groups of longitudinal smooth muscle fibres occur dorso-medial to the coprodaeum, as was found in *P. melanotus*.

Intestine (Figure 44)

The intestine anterior to the coprodaeum displays internal folding and is lined with a pseudostratified columnar epithelium, consisting of columnar and some goblet cells, the same as observed in *P. melanotus*. The columnar epithelial cells contain oval nuclei with some round nuclei evident in some areas. The epithelium of the intestine shows apparent seasonal variation in height (see section 5.3 on seasonal variation). The layers which underly the intestinal epithelium is the same as observed for *P. melanotus*. A connective tissue layer is followed by an inner and an outer muscularis which are separated by a vascularized connective tissue layer. The composition and orientation of the muscularis layers are comparable to that of *P. melanotus*. The inner muscularis consists of two thin muscle fibre layers of which the inner muscle layer also extends into the luminal folds. The outer layer consists of circularly arranged

smooth muscle fibres and the inner muscle layer primarily of longitudinal muscle fibres with circularly arranged smooth muscle fibres evident on the inside of this layer in some areas. The outer muscularis consists of longitudinal smooth muscle fibres. External to the outer muscularis is a thin layer of connective tissue.

At the level of Figure 45 the beginning of the coprodaeum can be seen with some posterior blind ending cavities of the intestine dorsal and lateral to the ventro-medially located coprodaeum. The urinary bladder stalk is ventro-medial to the coprodaeum.

Urinary bladder stalk (Figure 46, level of Figure 45)

Anterior part - The wall of the urinary bladder stalk consists of the same three layers as described for the stalk of *P. melanotus*: a mucosa layer, a muscularis layer and a serosa layer.

The mucosa is composed of an inner pseudostratified columnar epithelium and an underlying connective tissue layer, the lamina propria. The columnar pseudostratified epithelium consists primarily of ciliated cells, but with a few unciliated mucous secreting cells also present, the same as observed in *P. melanotus*. The basal bodies which are associated with the ciliated cells stained intensively with azocarmyn. Small groups of longitudinal smooth muscle fibres are visible in the lamina propria which represent the muscularis mucosa. At the level where the coprodaeum begins the groups of longitudinal smooth muscle fibres (muscularis mucosa) in the lamina propria of the urinary bladder stalk are more concentrated ventrally and dorso-medially.

The muscularis layer, external to the lamina propria, consists of circularly arranged smooth muscle fibres with some longitudinally arranged ones present external to the circularly arranged ones in some regions. The serosa on the outside of the muscularis consists primarily of vascularized connective tissue.

Urogenital ducts (level of Figure 45)

Uteri (Figure 47)

As in *P. melanotus* the uteri in this region are lined with columnar ciliated epithelia, which is thrown into folds (plicae) of which the the epithelium exhibits cripts. Vascularized connective tissue, the lamina propria, extends into every fold and is followed by a layer of circularly arranged smooth muscle fibres, the same as observed in *P. melanotus*. External to the circularly arranged muscle layer, in some areas, are bundles of longitudinal smooth muscle fibres, embedded in connective tissue.

Ureters (Figure 48)

The ureters have positions dorsal to the uteri and are lined with columnar epithelial cells with round, basal nuclei.

Coprodaeum (Figure 49)

At the point where the coprodaeum begins (see Figure 45), the intestine is present as posterior blind ending cavities dorsal and lateral to the ventro-medially located coprodaeum. The coprodaeum is lined by a columnar epithelium consisting of mucous secreting cells with basal nuclei. A connective tissue layer underlies the coprodaeum epithelium. The epithelium and its underlying layer of connective tissue (lamina propria) represent the mucosa of the coprodaeum. The connective tissue layer is followed by an inner- and an outer muscularis, as was observed in *P. melanotus*. The inner muscularis of the coprodaeum is more developed than that of the terminal intestine, consisting primarily of circularly arranged smooth muscle fibres with some longitudinal muscle fibres intermingled with the circular muscle fibres in some areas. The outer muscularis forms the lateral borders of the coprodaeum and the intestinal cavities and consists of groups of longitudinal smooth muscle fibres. A vascularized connective tissue layer, which is thicker in the lateral regions, separates the inner- and the outer muscularis. Numerous blood migrants are

visible in this connective tissue. External to the outer muscularis is a thin layer of vascularized connective tissue, which represents the serosa layer.

The epithelium of the coprodaeum is infected by protozoan parasites similar to those found in *P. melanotus* in the same region.

4.1.2.2. **Region 2** (see Figure 2)

This region encompasses the rest of the coprodaeum, the urodaeum, the urinary bladder stalk and the urogenital ducts. The urogenital ducts join the cloaca in this region.

Urodaeum

At the level of Figure 50 the intestinal cavities have already terminated, with the urodaeum now evident dorsal to the coprodaeum, as more than one urodaeal cavities of the two anterior urodaeal limbs. The urodaeal cavities are lined with stratified columnar epithelium, 2-5 cells in thickness with apical mucous secreting cells (Figure 51) as was the case in *P. melanotus*. The epithelial lining of the urodaeum shows seasonal variation in secretory activity (see section 4.3. on seasonal variation). Urodaeal glands occur in the walls of the urodaeal limbs. These glands contains columnar epithelia with mucous secreting cells and are tubular, branched and exocrine (Figure 51). In one female these glands have shown seasonal regression, which may be correlated with the reproductive cycle (see section on seasonal variation). Ventral to the urodaeal limbs is a layer of circularly arranged smooth muscle fibres, separated from the circularly arranged muscle fibres of the coprodaeum by means of a thin connective tissue layer. Posteriorly (Figure 52), the anterior urodaeal limb cavities have coalesced to form a common urodaeal cavity. The epithelia of the urodaeum and the urodaeal glands are infected by protozoan parasites as was

the case in *P. melanotus*. A common wall exists between the urodaeum and the coprodaeum at this level which is largely composed of transversely and circularly arranged smooth muscle fibres.

Urinary bladder stalk.

Near the junction with the coprodaeum the columnar epithelium of the urinary bladder stalk coasists primarily of unciliated cells, similar to the situation in *P. melanotus*. At the level of Figure 53 the urinary bladder stalk opens into the coprodaeum, anterior to the coprodaeum-urodaeum junction. In this specimen the lumen of the urinary bladder stalk anterior to its connection with the coprodaeum, is reduced. The junction between the urinary bladder stalk and the coprodaeum is anteriorly in the form of a short canal in a medial position. Posteriorly, this junction enlarges. In one female specimen examined (Figure 54) the urinary bladder stalk and the coprodaeum merge by means of a relatively long passageway, at a level where only the anterior urodaeal glands are evident. This junction is comparable with the above described junction described above between the urinary bladder stalk and the coprodaeum. In yet another female specimen examined the urinary bladder stalk merges with the coprodaeum in a medial position over a relatively short distance. In another specimen examined, the urinary bladder stalk which extends posteriorly as blind ending cavities, ventral to the coprodaeum-urodaeum cavity (Figure 55). These cavities terminates at the level where the proctodaeum begins. The junction between the urinary bladder stalk and the cloaca can also be posterior to the coprodaeum-urodaeum junction (Figure 56).

Posterior to the coprodaeum-urinary bladder stalk junction, a passageway is formed between the coprodaeum and the urodaeum (Figure 59). More posteriorly (Figure 60) a much enlarged coprodaeum-urodaeum cavity exists.

Urogenital ducts

Uteri - Posteriorly, the vascularized lamina propria of the uteri contains groups of longitudinal smooth muscle fibres (muscularis mucosa) which are more concentrated on the ventral and lateral sides (Figure 57). The uteri empti into the urodaeal cavity (see figure 59).

Ureters

The luminal linings of the ureters change to taller mucous secreting cells near its junction with the cloaca (Figure 58).

The ureters empty through the dorsal wall (urodaeum part) of the coprodaeum-urodaeum cavity at this level.

4.1.2.3. Region 3

This region includes only the proctodaeum.

At the level of Figure 61 the coprodaeum-urodaeum cavity has become reduced, exhibiting a more folded luminal epithelium. This is an indication of the start of the third cloacal division, the proctodaeum. Located in a ventro-lateral position on each side of the proctodaeum is a blood plexus. The urodaeal glands at this point are restricted to the dorsal folds and a few to the lateral folds of the coprodaeum-urodaeum cavity. Located in a lateral position the first proctodaeum associated glands (dorsal glands) can be seen. In a ventro-medial position is the hypoischium with muscles fibres extending from it. In this specimen the beginning of the proctodaeum with its associated glands, is not well defined. However, in one of the other females examined, the proctodaeum has a medial position between the posterior coprodaeum-urodaeum cavities with which it was still connected (Figure 62). In another female specimen examined the beginning of the proctodaeum was in the form of a sphincter-like structure,

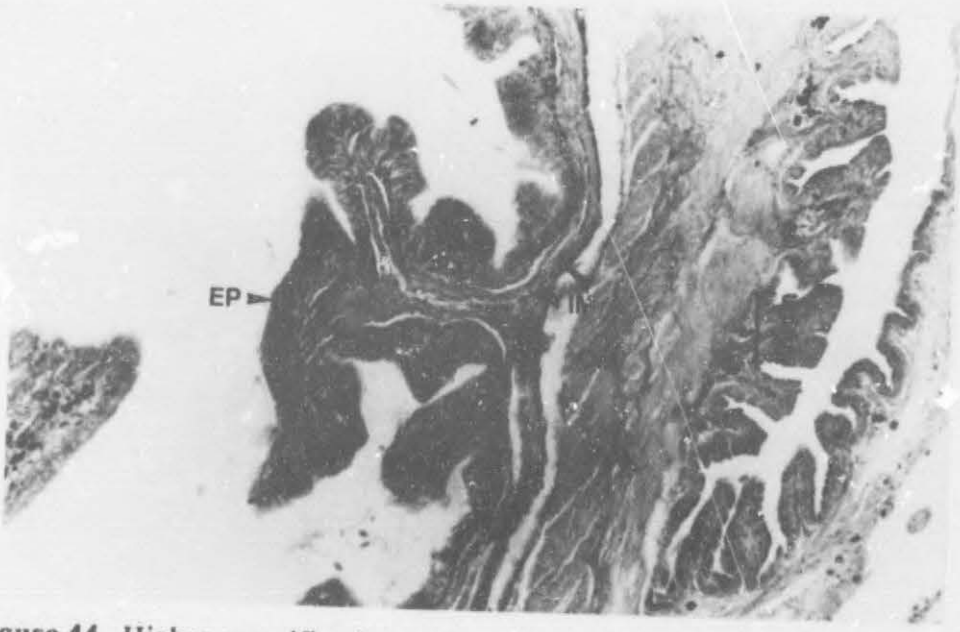

Figure 44. Higher magnification to show the consisting layers of the intestine. Note that the inner muscularis (IM) consists of two muscle fibre layers.

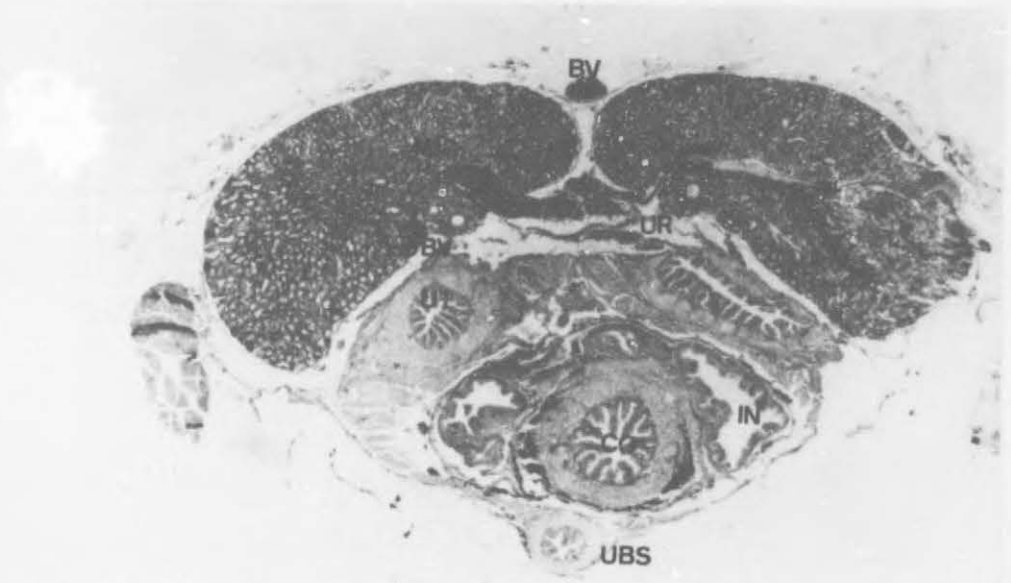

Figure 45. Section through the beginning of the coprodaeum (CO). Note the posterior blind ending cavities of the intestine (IN). Also note the positions of the ureters (UR), uteri (UT) and urinary bladder stalk (UBS).

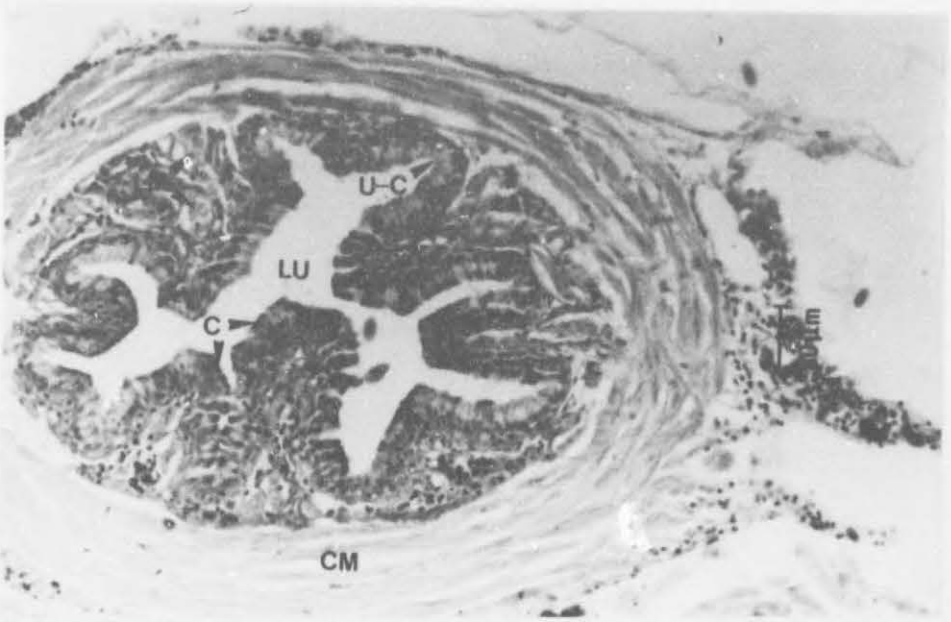

Figure 46. Higher power view (x20) of the anterior urinary bladder stalk to show the consisting layers. C=cilia; CM=circularly arranged muscle fibres; CT=connective tisue; LU=lumen; U-C=unciliated cells.

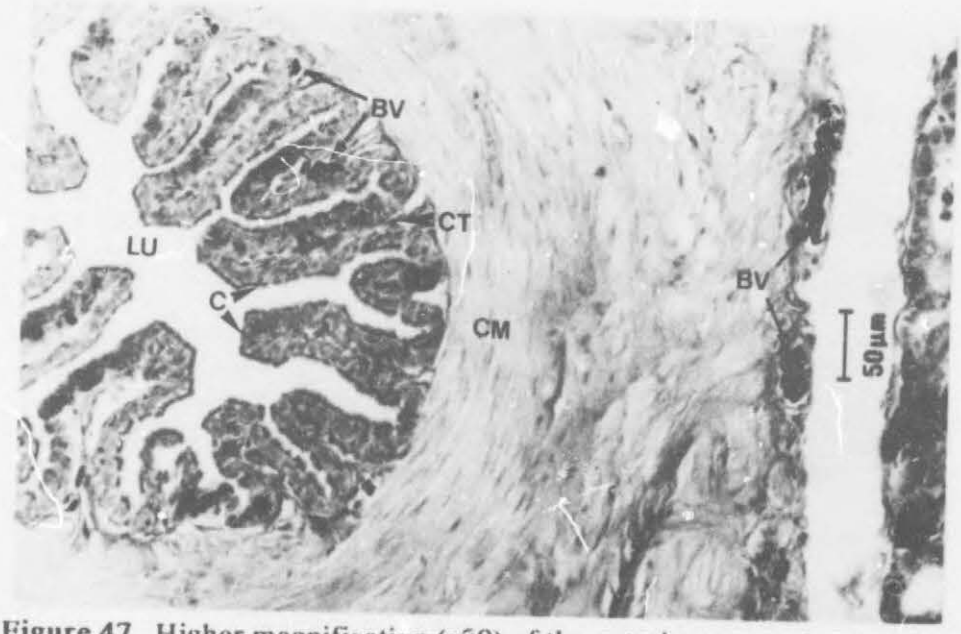

Figure 47. Higher magnification (x20) of the anterior uterus showing the consisting layers. BV=blood vessels; LU=lumen; C=cilia; CM=circularly arranged smooth muscle fibres; CT=connective tissue.

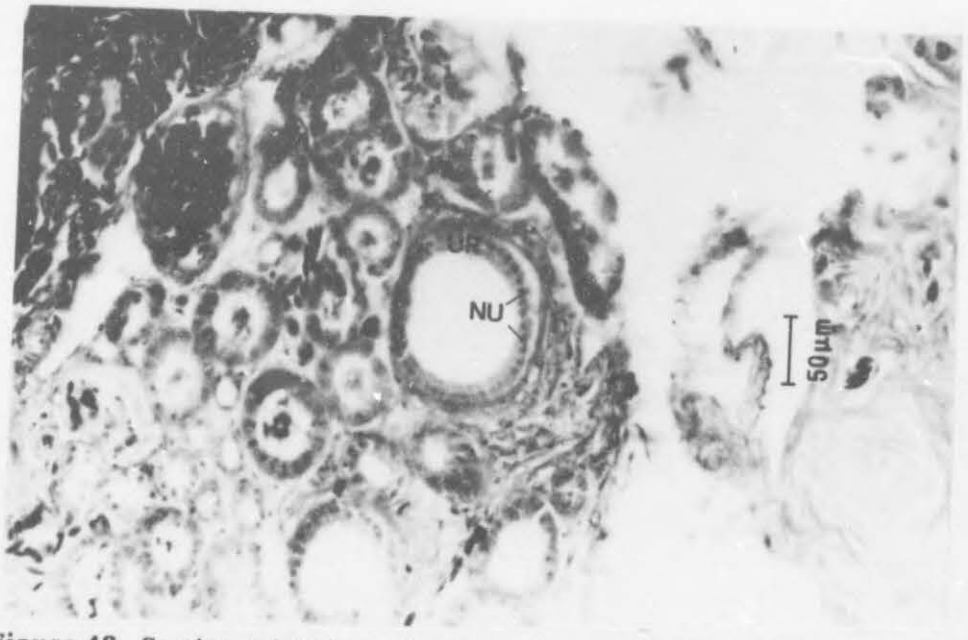

Figure 48. Section (x20) through a anterior ureter (UR) to show its luminal epithelium. NU=nuclei.

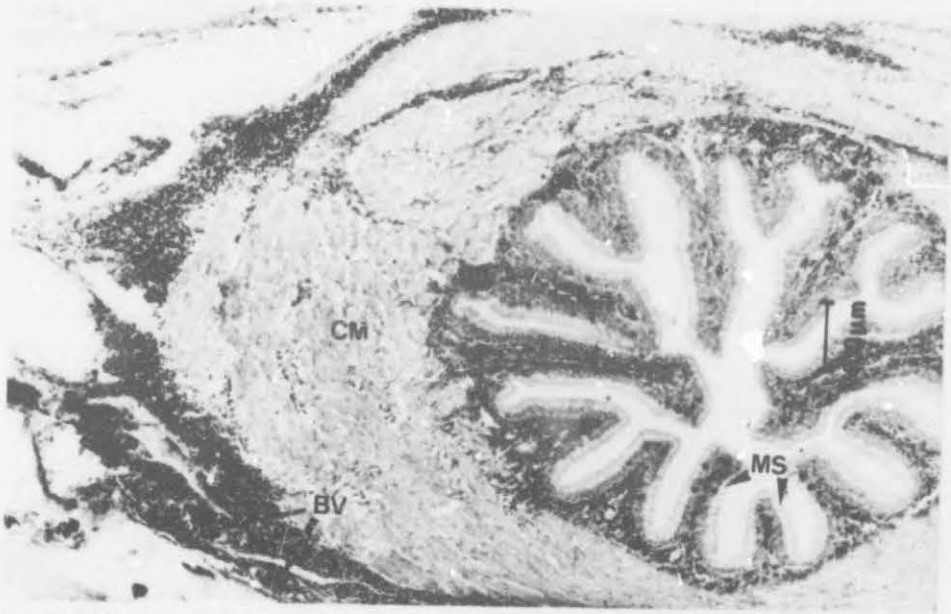

Figure 49. Section (x10) through the coprodaeum to show the underlying layers of the epithelium. Note the protozoan parasites in the epithelium. BV=blood vessels; CT=connective tissue; CM=circularly arranged muscle fibres; MS=mucous secreting cells.

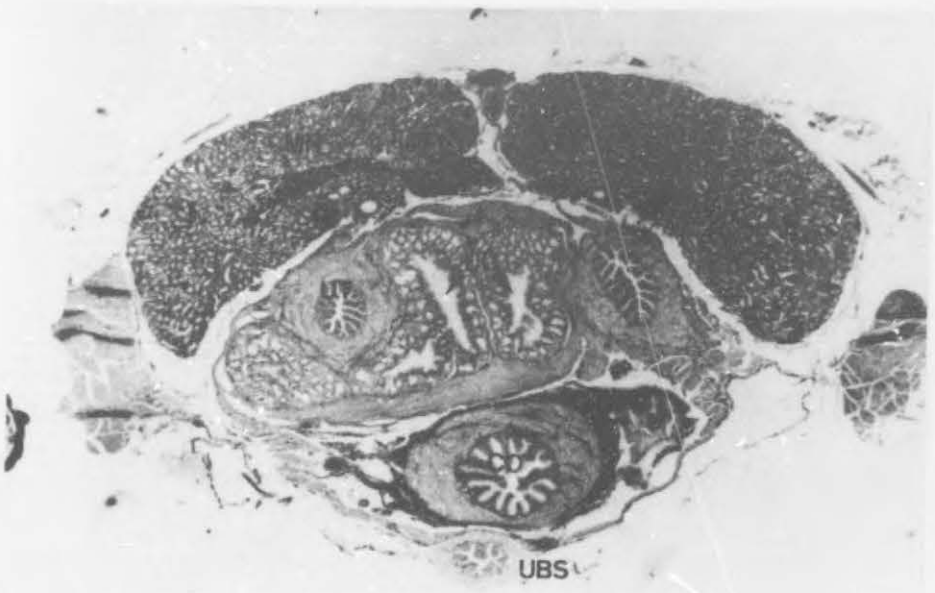

Figure 50. Section through the coprodaeum (CO) and the anterior urodaeal limbs. Note the urodaeal glands (UG) in the urodaeal limb walls. MN=metanephros; UBS=urinary bladder stalk; UC=urodaeal cavities; UT=uterus; .

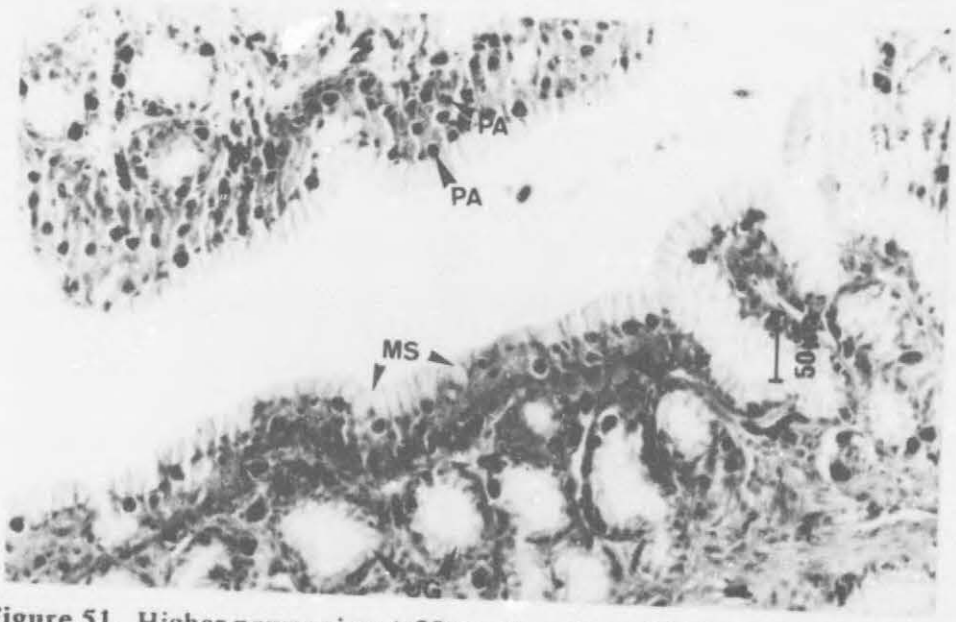

Figure 51. Higher power view (x20) to show the epithelium of the urodaeum and the urodaeal glands. Note the parasites (PA) in the urodaeal and urodaeal gland epithelia. MS=mucous secreting cells.

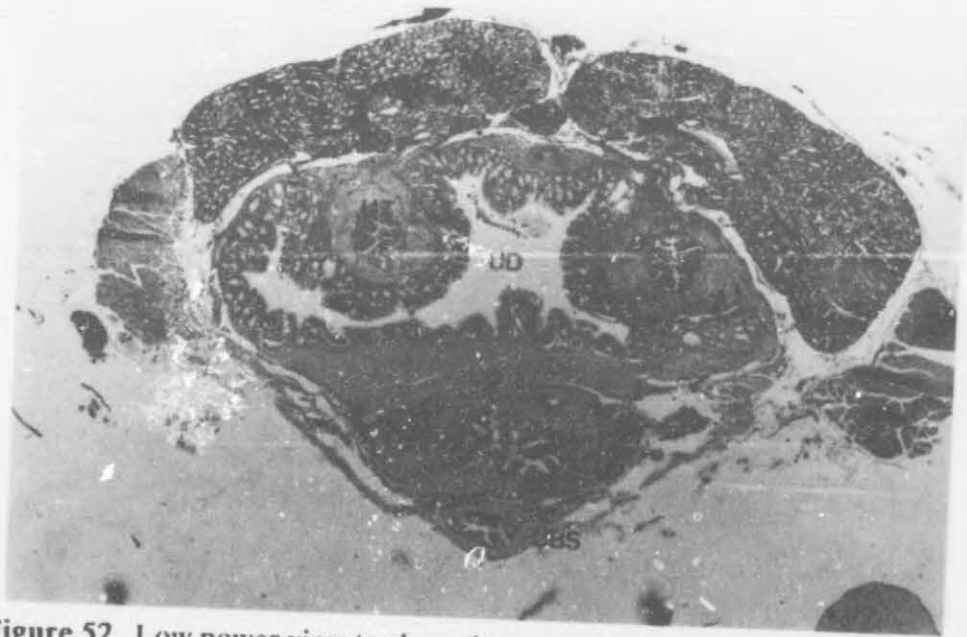

Figure 52. Low power view to show the common urodaeal cavity (UD) and the common wall between the coprodaeum (CO) and urodaeum (UD). UC-W=urodaeum-coprodaeum wall; UBS=urinary bladder stalk.

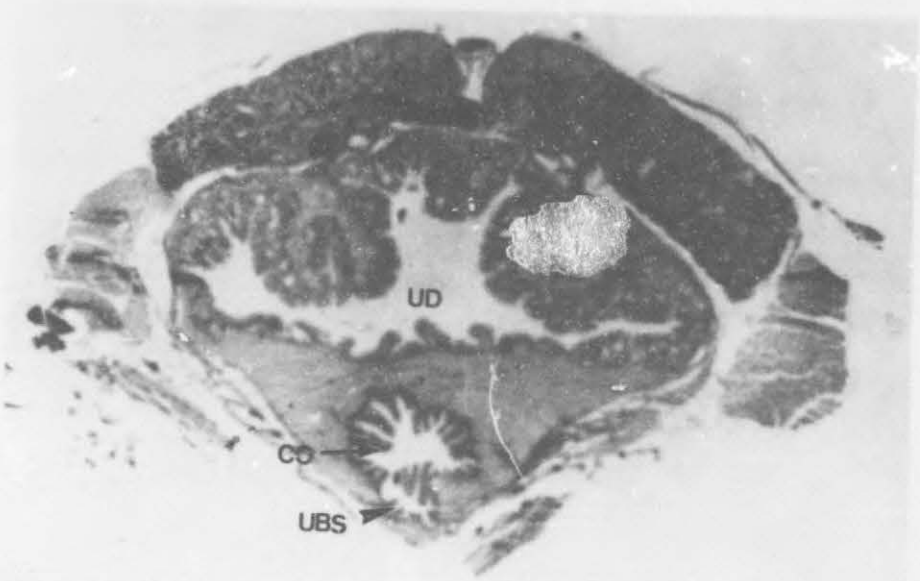

Figure 53. Low power view of the cloacal complex to show the junction between the urinary bladder stalk (UBS) and the coprodaeum (CO).

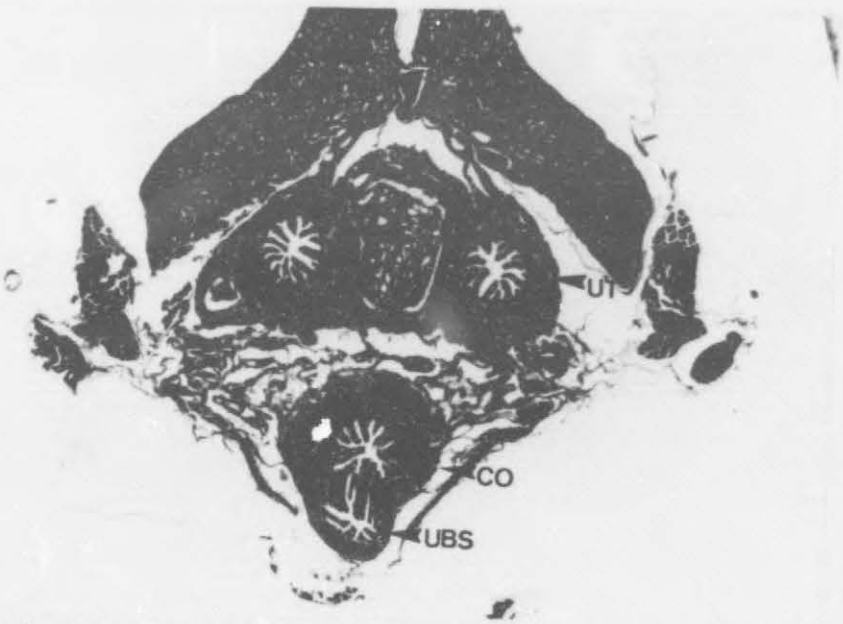

Figure 54. Low power view to show the junction between the urinary bladder stalk (UBS) with the coprodaeum at the level where only the anterior urodaeal glands (UG) of the urodaeum are evident.

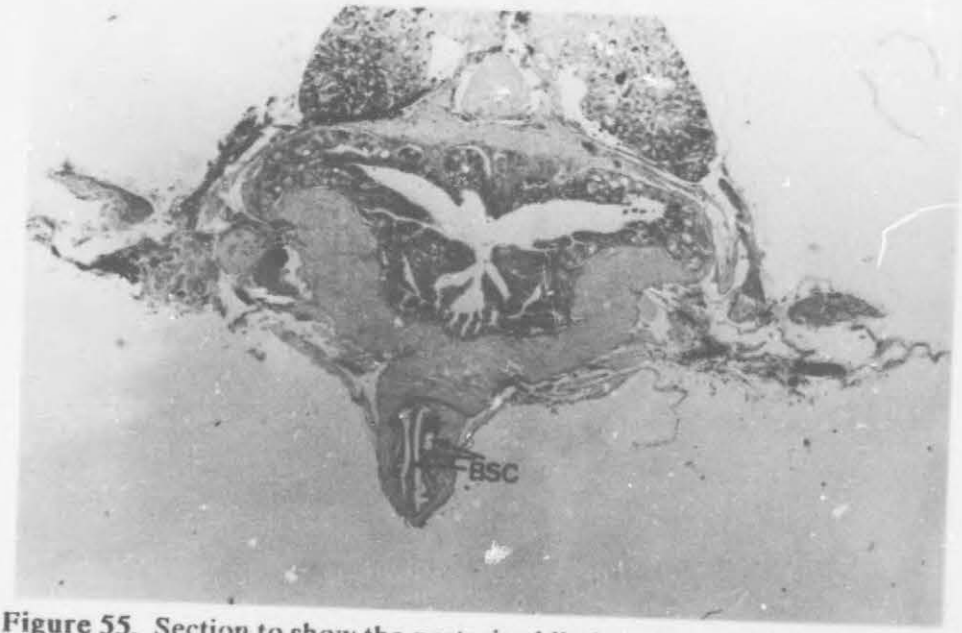

Figure 55. Section to show the posterior blind ending cavities of the urinary bladder stalk (arrow) posterior to its connection with the cloaca.

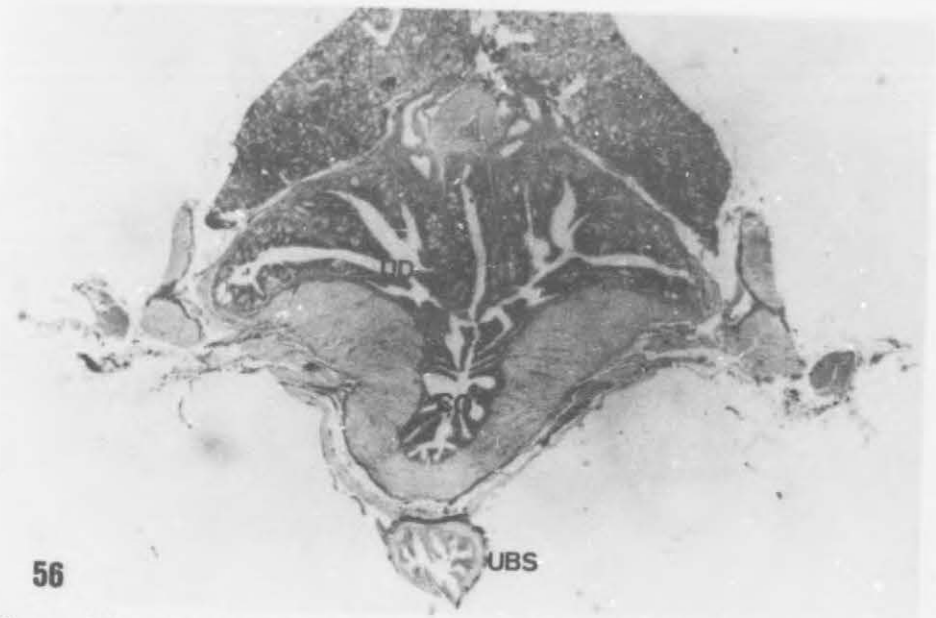

Figure 56. Low power view of the cloacal complex to show the junction between the coprodaeum and the urodaeum anterior to the bladder stalk-coprodaeum junction.

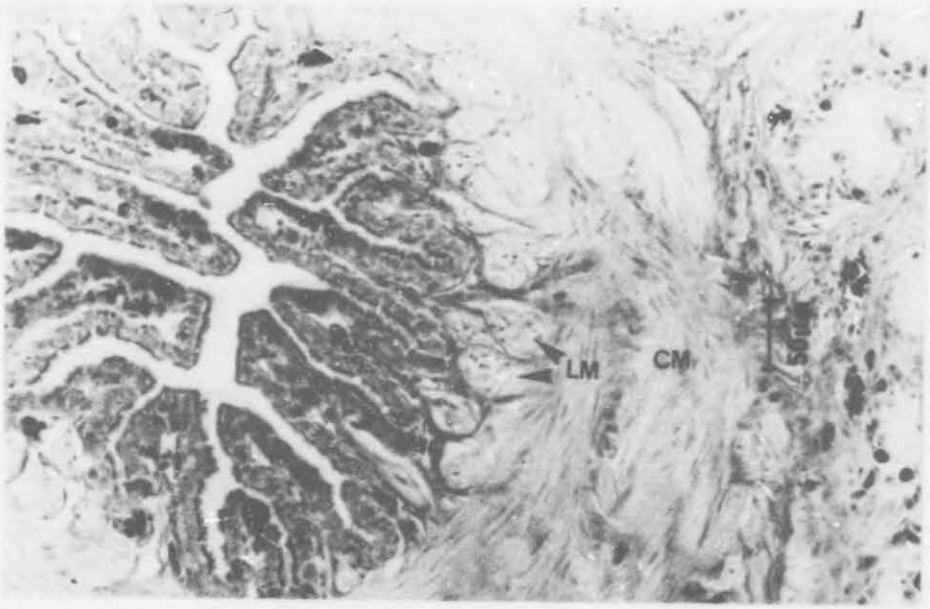

Figure 57. Section (x20) through the posterior uteri to show the groups of longitudinal muscle groups (LM) in the connective tissue which underly the epithelium. CM = circularly arranged muscle fibres.

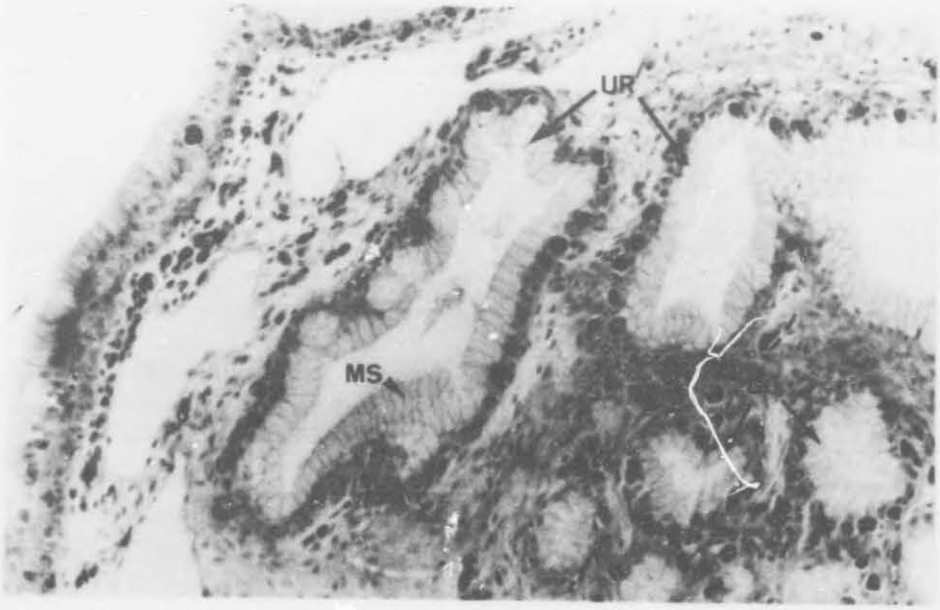

Figure 58. Section through the posterior ureter showing its luminal epithelium (Ep). MS = mucous secreting cells; UG = urodaeal glands.

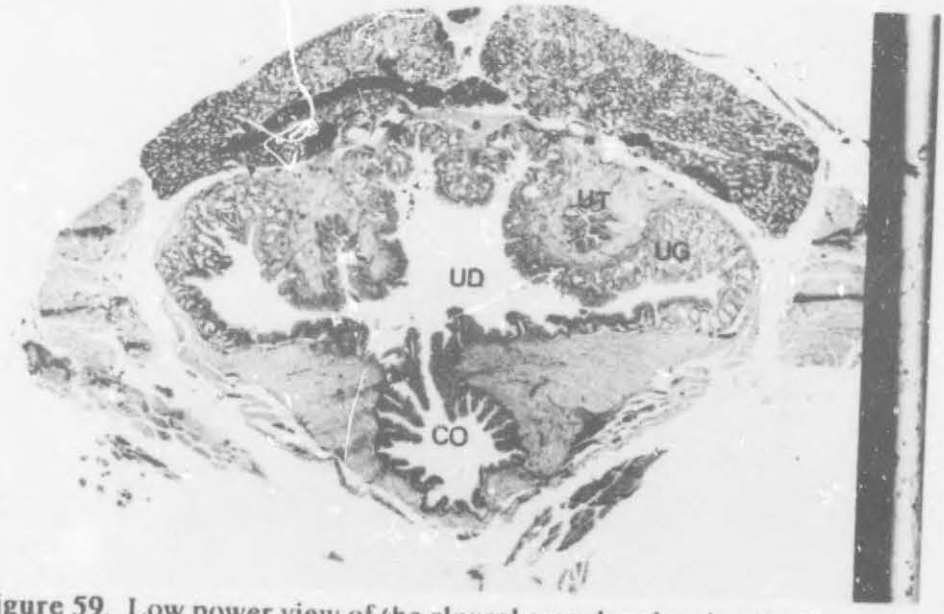

Figure 59. Low power view of the cloacal complex showing the junction (arrow) between the coprodaeum (CO) and the urodaeum (UD). Note that the one uterus (UT) empty into the urodaeum at this level. UG = urodaeal glands.

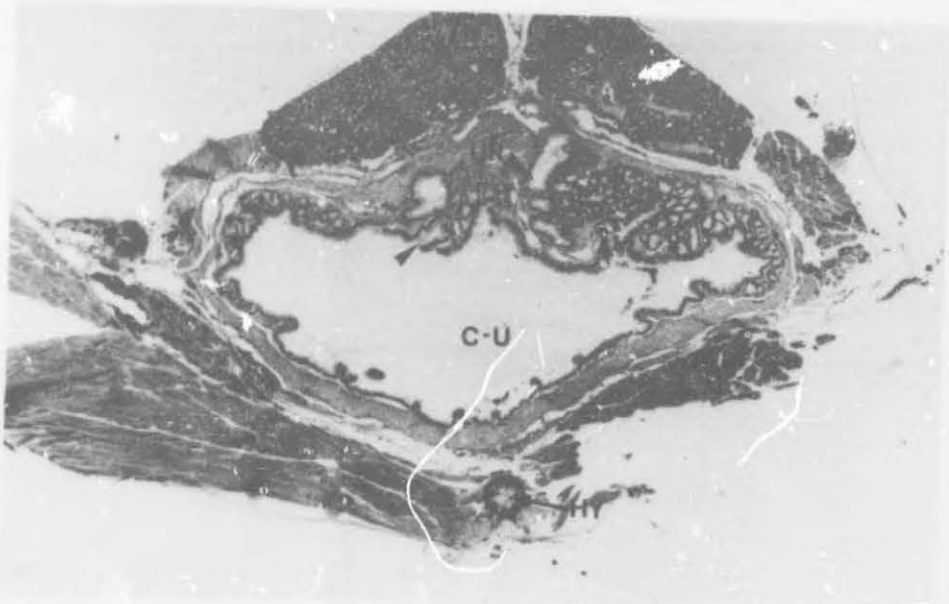

Figure 60. Section through the coprodaeum-urodaeum (C-U) to show the junction between the ureters (UR) and the cloaca (arrow). UG = urodaeal glands; HY = hypoischium.

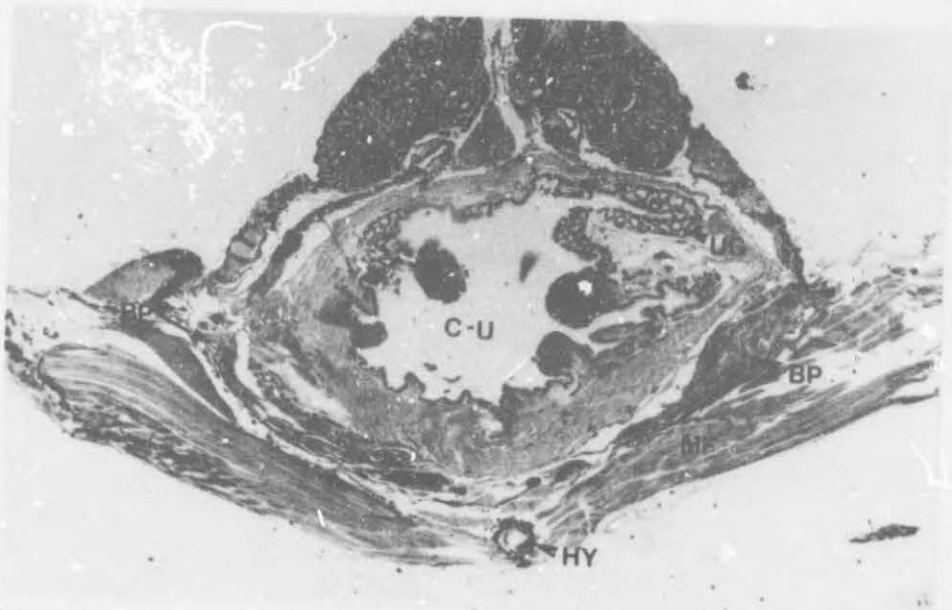

Figure 61. Low power view of the cloacal complex showing the reduced lumen of the coprodaeum-urodaeum cavity (C-U), indicating the start of the proctodaeum. Note the reduced number of urodaeal glands (UG) and the first group of ventral glands (VG). BP=blood plexus.

Figure 62. Section (low power) to show the anterior proctodaeum (PR), in the form of a sphincter, which is still in connection with the coprdaeum-urodaeum cavities (C-U).

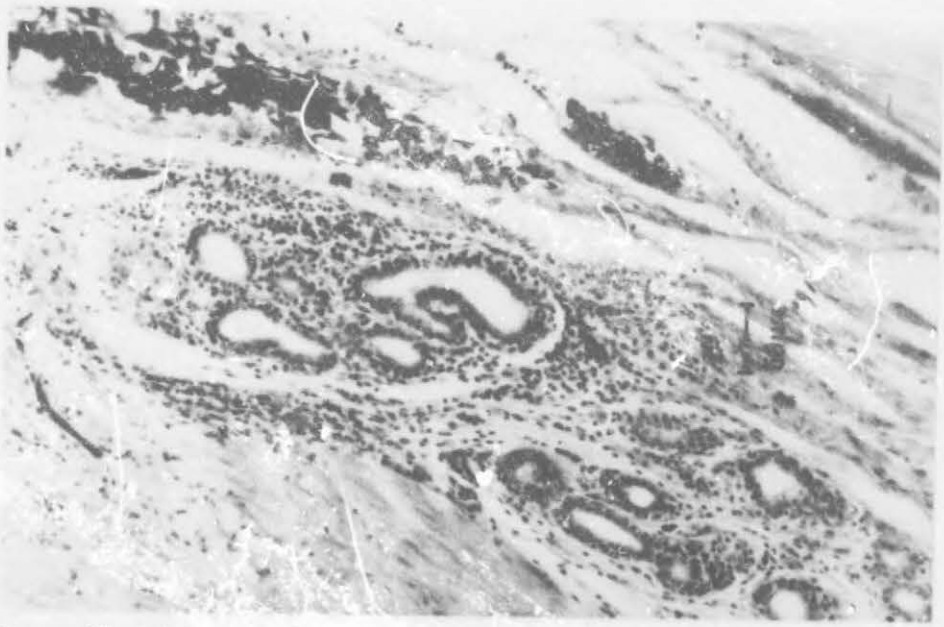

Figure 63. Higher power view (x20) to show the reduced lumina of the ventral glands (VG).

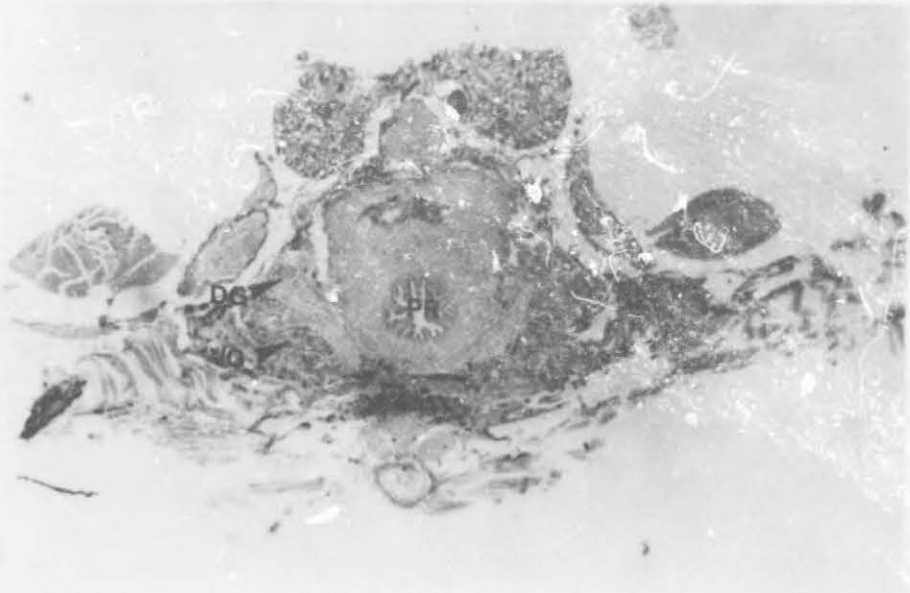

Figure 64. Section through the proctodaeum (PR) showing the dorso-lateral dorsal glands (DG) and the ventro-lateral ventral glands (VG).

Figure 65. Higher magnification (x10) to show the cornified, stratified epithelial lining (EP) of the proctodaeum near the vent. Note the cornification (CR) of the epithelium.

with dorsal and ventral glands located as paired structures on each lateral side (Figure 64). These dorsal- and ventral glands are tubular, branched and exocrine (Figure 63). These glands are more reduced in size than that found in *P. melanotus*. Because of the reduced lumina of the glands the type of cells in the epithelia are not so apparent. Near the vent the epithelium of the proctodaeum changes to a cornified stratified epithelium (Figure 65).

4.2. MALE

4.2.1. Gross anatomy (see Figure 22)

The gross anatomy of the male is basically the same as for the female with some structural variations especially in the urodaeum. As was the case in *P. melanotus* the urodaeum in males do not have anterior urodaeal limbs. As in the females the urinary bladder stalk connects the urinary bladder with the coprodaeum-urodaeum part of the cloaca ventrally. The ureters and the vasa deferentia run posteriorly ventral to the metanephros and open conjointly into the dorsal wall of the cloaca.

4.2.2 Microanatomy

As was done for the females the cloacal complex is, for description purposes, divided into three regions (see Figure 22). Figures 66 to 86 are transverse sections of the cloacal complex of a male *C. cordylus* (JEM 352, not spermiogenic active) with some variations as observed in the other male specimens examined, included.

4.2.2.1. Region 1 (see Figure 22)

This region includes the terminal intestine, the anterior urinary bladder stalk and the urogenital ducts.

Intestine

The terminal part of the intestine consists of the same layers as were described for the intestinal cavities in females (see Figure 44). The urinary bladder stalk and the coprodaeum also possess the same layers as described for the female (see Figures 46 and 49). Dorsal to the intestine, in a medial position, is a prominent group of longitudinal smooth muscle fibres which is in close association with blood vessels and nerve tissue (Figure 66). Lateral to this prominent muscle bundle are the vasa deferentia and the ureters.

Urogenital ducts

Vasa deferentia - The lumina of the vasa deferentia are reduced in this section and are lined with cubical epithelial cells (Figure 66). Each vas deferens is surrounded by a relatively thin circularly arranged smooth muscle fibre layer.

Ureters - The ureters are lined with simple columnar epithelia consisting of secreting cells (Figure 66).

4.2.2.2. **Region 2** (see Figure 22)

This region encompasses the coprodaeum, the urodaeum, the urinary bladder stalk and the urogenital ducts. At the level of Figure 67 the coprodaeum exhibits a position ventral to the enlarged intestine.

Urinary bladder stalk - At the level of Figure 68 the muscle layers of the coprodaeum and the urinary bladder stalk are consolidated, with a posterior blind ending cavity of the intestine still visible. A passageway between the coprodaeum and the urinary bladder stalk, anterior to the urodaeum-coprodaeum connection, can be seen. This passageway is in a medial position and posteriorly the junction between the urinary bladder stalk and coprodaeum enlarges. In this specimen the urinary bladder stalk lumen has no direct

connection with the urodaeum lumen. However, in another male specimen examined, the urinary bladder stalk merged with the coprodaeum and the urodaeum at more or less the same level (Figure 69). In the latter male specimen the lumen of the urinary bladder stalk becomes flattened and extends posteriorly lateral to the coprodaeum to find junction with the urodaeum dorsal to the coprodaeum. At more or less the same level the urinary bladder stalk opens into the coprodaeum in a medial position.

Urodaeum

The start of the urodaeum as cavities dorso-lateral to the coprodaeum is evident in this section (Figure 68). Posteriorly, these urodaeal cavities coalesce to form a common urodaeal cavity. The urodaeal lumen is lined by columnar epithelial cells which are secretory in some areas. The urodaeum joins the coprodaeum posteriorly by means of an enlarged junction (Figure 70) to result in a coprodaeum-urodaeum cavity.

Urogenital ducts

At the level of Figure 70 the ureters are dorso-lateral on the inside of the vasa deferentia. The muscle layer which surrounds the vas deferens is more developed at this level. On each side, the vas deferens joins the ureter anterior to their conjoint junction with the coprodaeum-urodaeum cavity (Figure 71). The junction of the urogenital ducts with the cloaca is in more or less the same position as where the ureters of females empty into the cloaca.

4.2.2.3. Region 3 (see Figure 22)

This region includes the proctodaeum.

At the level of Figure 72 the coprodaeum-urodaeum cavity exposes a sphincter, which indicates the beginning of the proctodaeum. Also evident in this section are posterior blind ending cavities of the coprodaeum-urodaeum cavity. At this point a blood plexus can be seen on both sides of the proctodaeum. Groups of ganglion cells are now present ventro-lateral to the prominent longitudinal smooth muscle fibre bundle. Some dorsal and ventral glands are evident on the one side of the proctodaeum. At the level of Figure 73, these glands are present dorso-laterally (dorsal glands) and ventro-laterally (ventral glands) on both sides of the proctodaeum. The proctodaeum epithelium consists of columnar secretory cells (Figure 74) and rests on a fairly thick vascularized connective tissue layer (lamina propria). The outer muscularis is now reduced to two longitudinal groups in a ventro-medial position. The dorsal and ventral glands are embedded in connective tissue external to the inner muscularis. These glands are much more prominent in the males than in females and are tubular, branched and exocrine, as in the females. Mucous cells are present in the epithelium of these glands, but it is not certain if serous cells are also present (Figure 75). At the level of Figure 76 the lumen of the proctodaeum is more flattened after it has found junction with two laterally located cavities which are lined with non-secretory cubical cells. A relatively thick connective tissue layer, infiltrated with red staining blood migrants, is evident in a position ventro-medial to the proctodaeum. The ventral inner muscularis layer of the proctodaeum is lacking in this section. The proctodaeum wall is now dominated by the dorsal and ventral glands. Posteriorly (Figure 77), the dorsal and the ventral glands extend to positions ventro- and dorso-medial to the proctodaeum with a reduction in the number of ventral glands. The proctodaeum epithelium changes to a stratified squamous one with the dorsal epithelium still lined with

non-secretory cubical cells (Figure 78). At this level the dorsal glands empty into the proctodaeal cavity. Near the vent the ventral glands are lacking with some dorsal glands still evident in the proctodaeum wall. The ventral surface of the proctodaeum is cornified at this level (Figure 79).

4.3. SEASONAL VARIATION

No final conclusions regarding seasonal variation in the anatomy of the cloacal complex can be drawn because too few animals have been examined. No specific seasonal variation in any of part of the cloacal complex could be established for males except for the height of the intestinal epithelium. As in *P. melanotus*, more animals should be investigated to establish if this variation in thickness of the intestine epithelium is not the result of intraspecific variation.

The following variations were found in the females which seems to be correlated with the reproductive cycle.

1. Intestine anterior to cloaca

The luminal lining of the intestine shows seasonal variation in height. The specimens collected in January (FB 430) and in April (FB 1510) display low intestinal epithelia while the specimens collected in October (FB 165), November (FB 1347) and July (FB 46) possessed taller intestinal epithelia.

2. Urodaeum

In the non-gravid specimens (Figure 80) the epithelial linings of the urodaeum is stratified and shows secretory activity. In the gravid females (Figure 81) the secretory activity of the urodaeal epithelium is lost. No apparent variation in the secretory activity of the urodaeal glands was observed among the specimens examined. However, in one gravid specimen (Figure 82) it was found that the luminal epithelium of the urodaeum was reduced in height and that the epithelia

of both the urodaeum the urodaeal glands have lost their secreting activity. In the latter specimen the luminae of the coprodaeum, urinary bladder stalk and the urodaeum were also reduced (Figure 92).

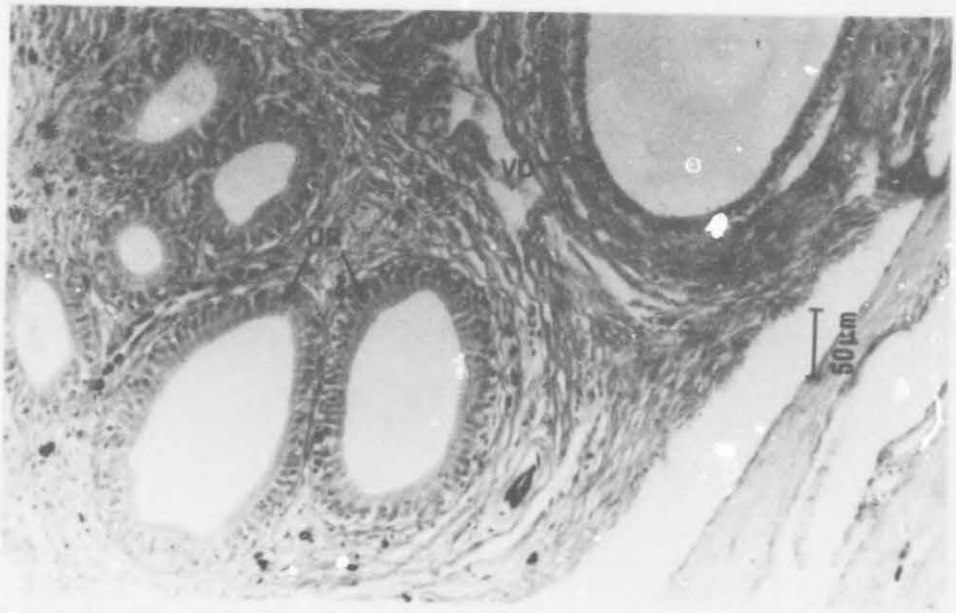

Figure 66. Section (x20) through the urogenital ducts dorsal to the intestine, to show their epithelia. VD=vas deferens; UR=ureter

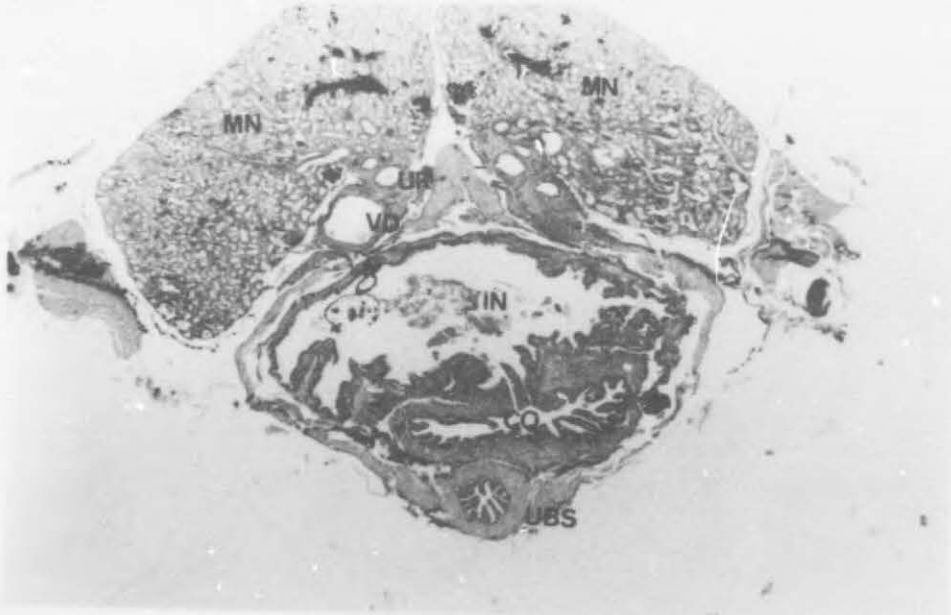

Figure 67. Low power view to show the beginning of the coprdaeum (CO) ventral to the intestine (IN). Note the positions of the ureters (UR), urinary bladder stalk (UBS) and the vasa d[illegible]rentia (VD). MN=metanephros

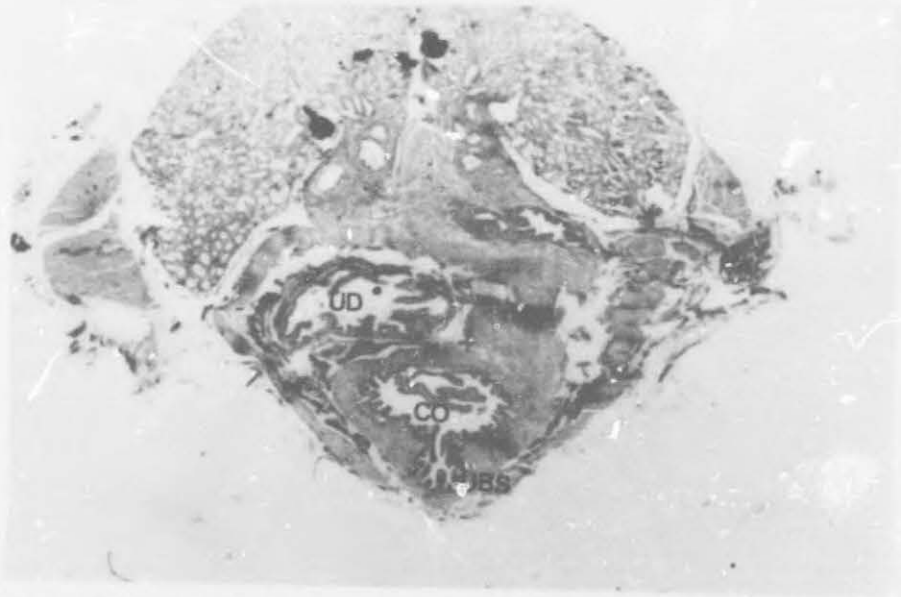

Figure 68. Low power view of the cloacal complex showing the junction between the urinary bladder stalk (UBS) and the coprodaeum (CO). Also take note of the first dorsal located urodaeal cavities (UD).

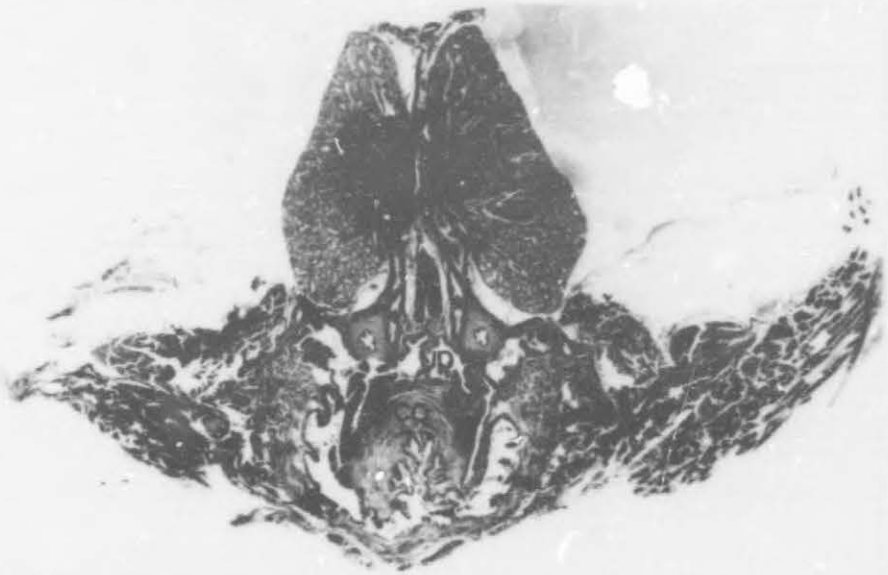

Figure 69. Low power view showing the connection of the urinary bladder stalk (UBS) with the coprodaeum (CO) and the urodaeum (UD) at more or less the same level.

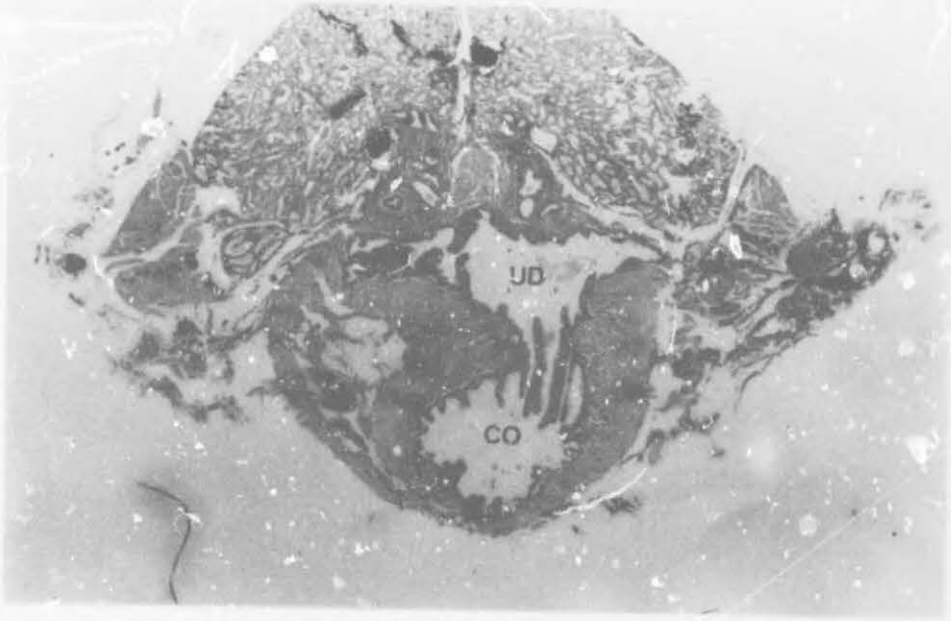

Figure 70. Section through the coprodaeum (CO) and urodaeum (UD) at the level where these two divisions merge (arrow). Note the lateral located blood plexus (BP) and ganglion (G) on the one lateral side. Also take note of the position of the ureters (UR).

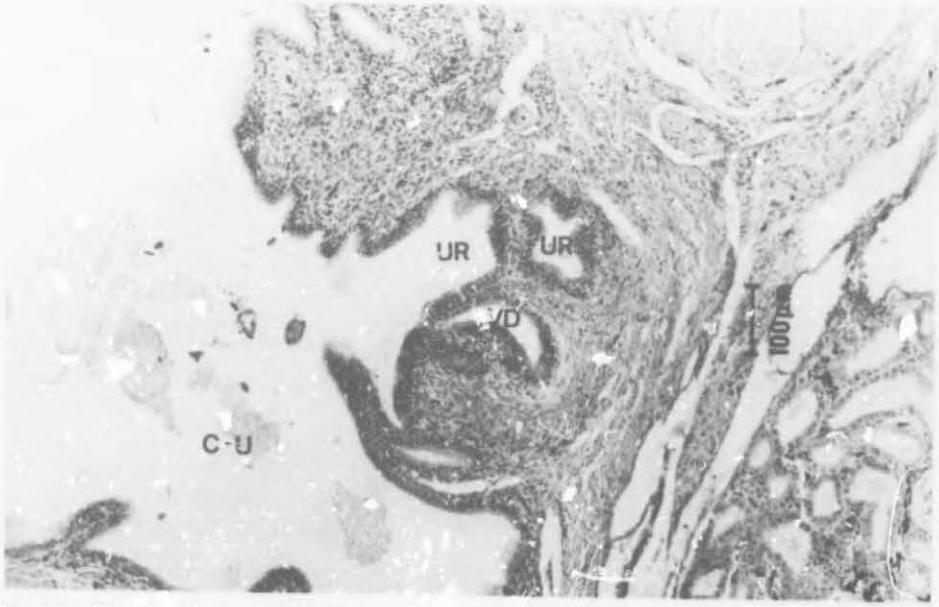

Figure 71. Section (x10) through the coprodaeum-urodaeum cavity (C-U) to show where the vasa deferentia (VD) and the ureters (UR) unite anterior to their connection with the cloaca.

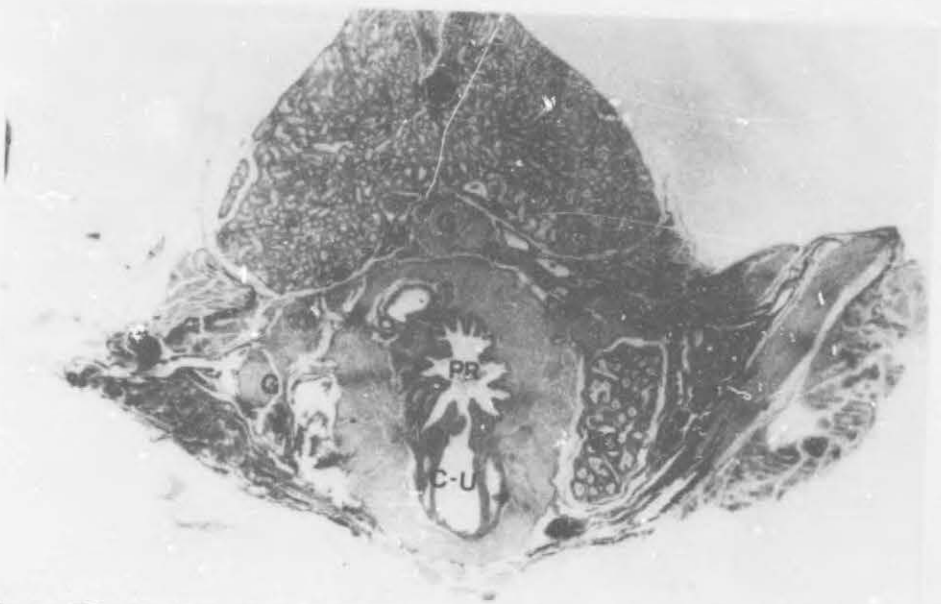

Figure 72. Section through the start of the the proctodaeum (PR). Note the posterior blind ending cavities of the coprodaeum-urodaeum cavity and the lateral located blood plexus (Bp) on each lateral side. G=ganglion cells; DG=dorsal glands; VG=ventral glands.

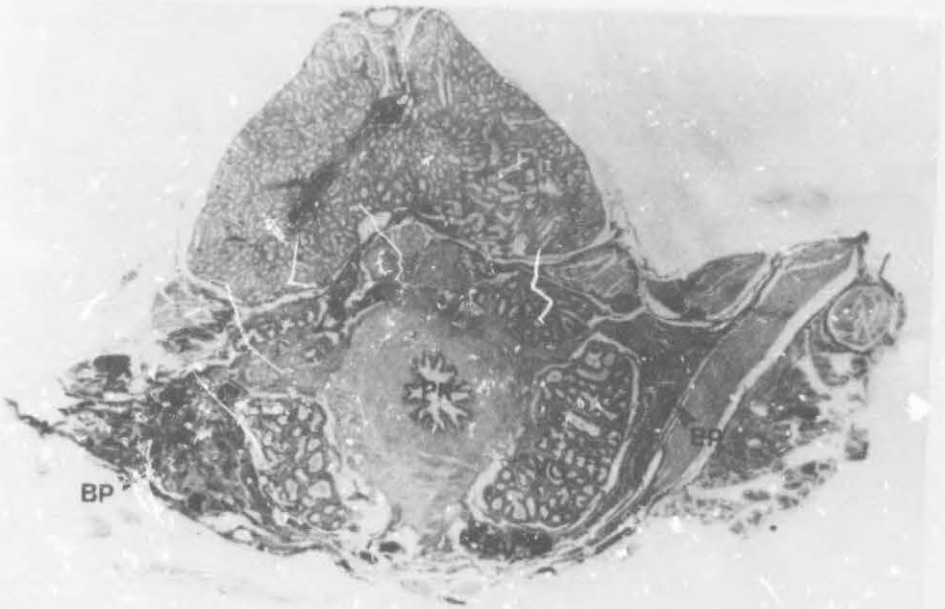

Figure 73. Section through the proctodaeum showing the dorsal- (DG) and ventral glands (VG) which dominate the proctodaeum wall. Also note the ganglion cell groups (G) ventro-lateral to the prominent longitudinal smooth muscle group (LM).

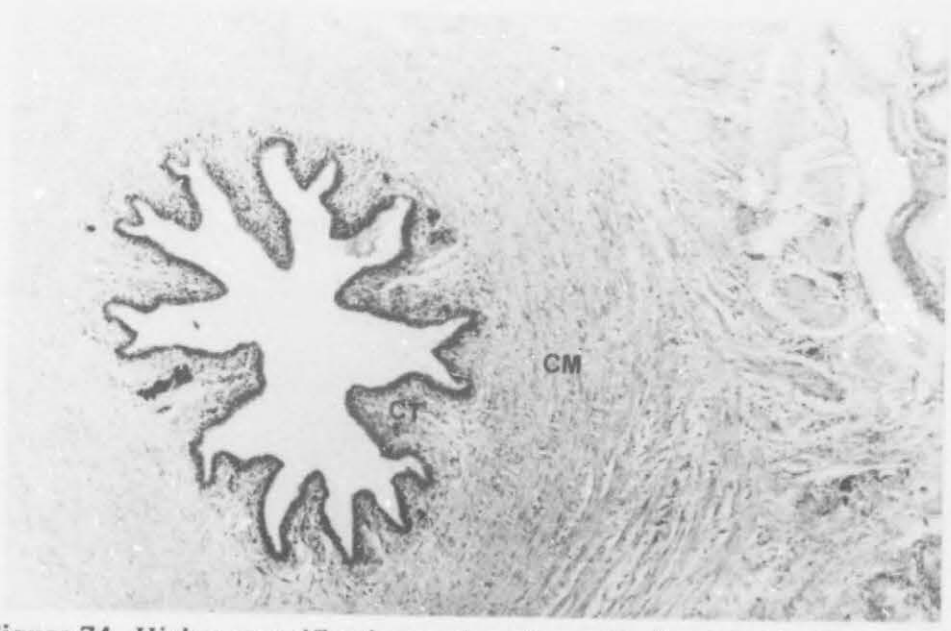

Figure 74. Higher magnification to show the epithelium of the proctodaeum and its underlying muscle layer. CT=connective tissue, CM=circularly arranged smooth muscle fibres.

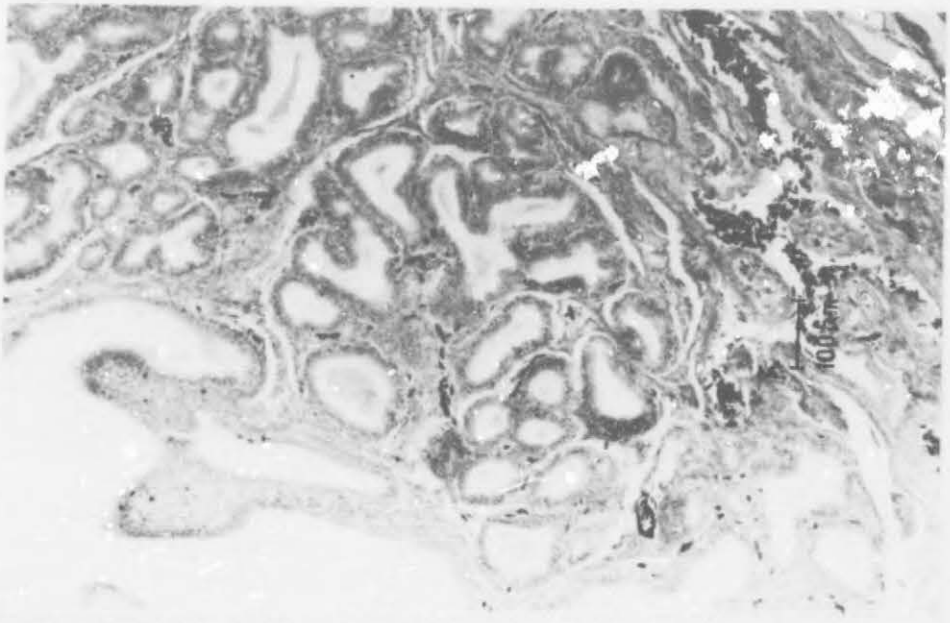

Figure 75. Section (x10) to show the luminal epithelia of the ventral and dorsal glands.

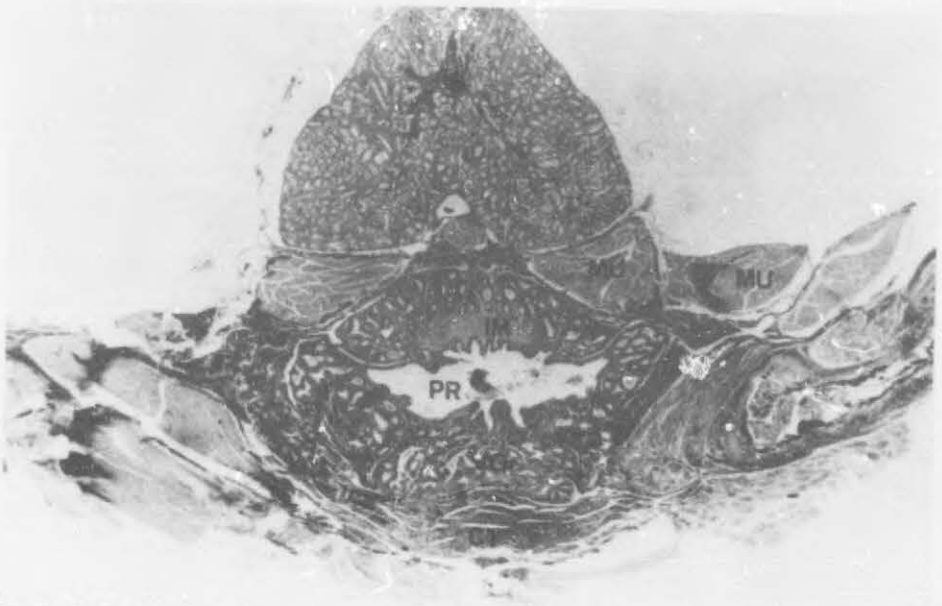

Figure 76. Section through the posterior part of the proctodaeum showing the flattened lumen. Take note of the relative thick ventrally located connective tissue (CT) and the conspcious dorsal- (DG) and ventral glands (VG) which now also locate medial positions. MU = muscle fibre groups.

Figure 77. Low power view of the cloacal complex to show reduced number of ventral glands (VG). DG = dorsal glands.

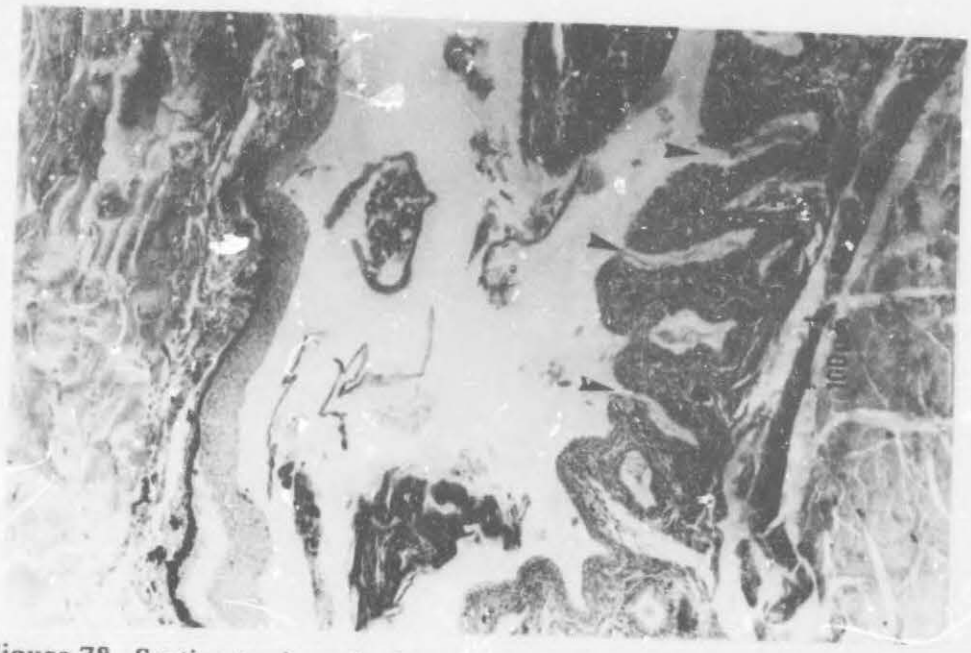

Figure 78. Section to show the luminal epithelia of the dorsal and ventral surface of the proctodaeum near the ve[illegible]. Note the squamous, stratified epithelium of the ventral luminal surface and the cubical epitelial cell lining of the dorsal luminal surface. Dorsal glands empty in[illegible]todaeum in this section (arrows).

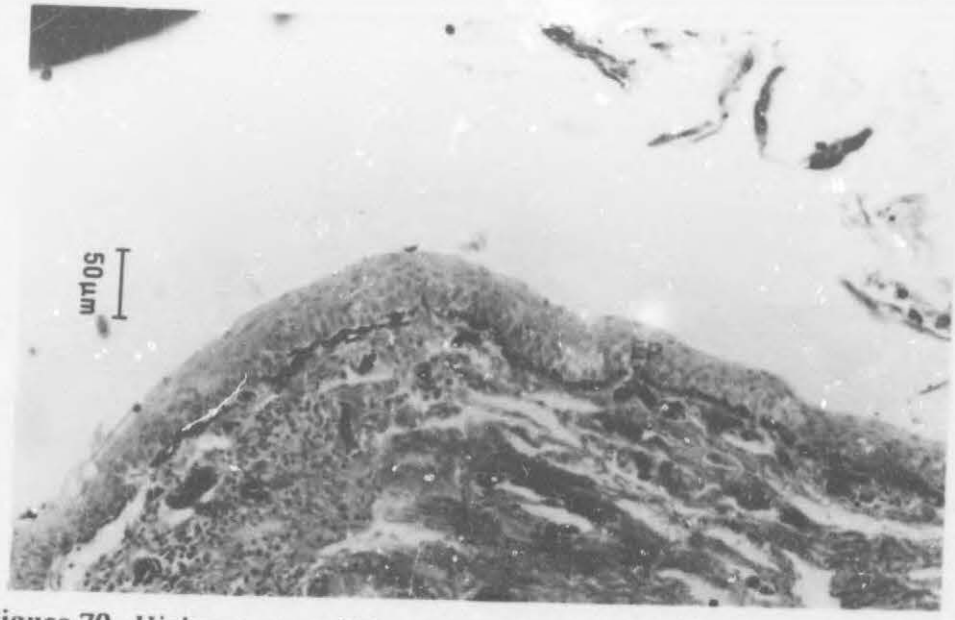

Figure 79. Higher power of Figure 77 to to show the squamous, stratified ventral epithelium of the proctodaeum near the vent.

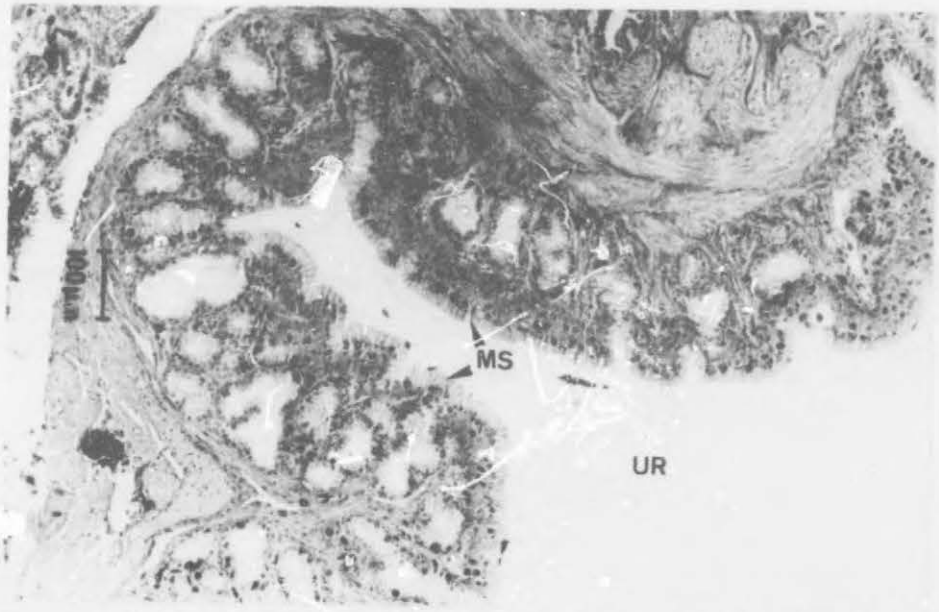

Figure 80. Section (x10) through the urodaeum in a non-gravid female, to show its luminal lining. Note that the apical epithelial cells are secretory. MS=mucous secretory.

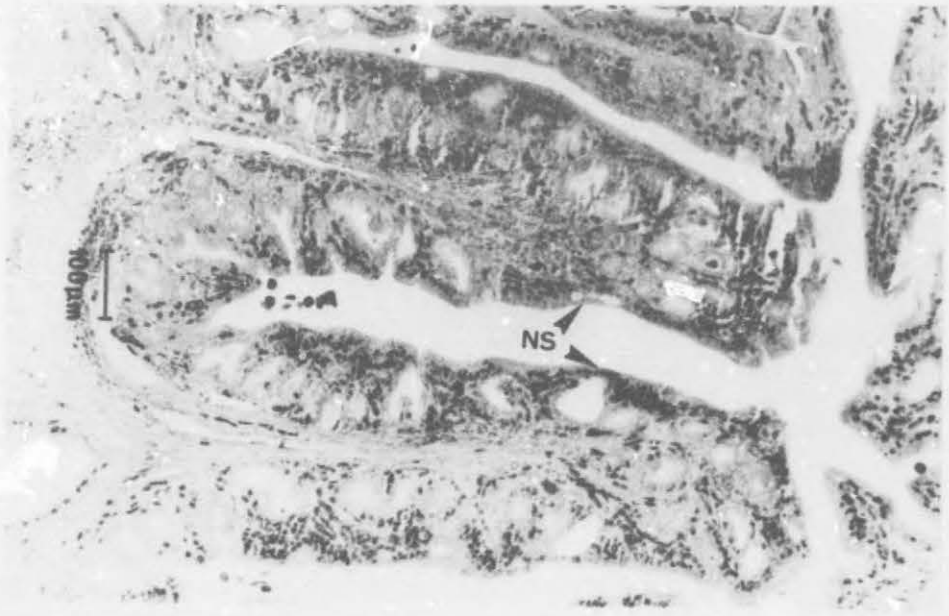

Figure 81. Section (x10) through the urodaeum in a gravid female. Note that the apical epithelial cells of the urodaeum are non-secretory..

CHAPTER 5

DISCUSSION

5.1. Cloacal division borders

Gadow (1887) was of opinion that the coprodaeum of the saurian cloacal complex is not well delimited and that the exact limit between the ectodermal proctodaeum and the endodermal parts (coprodaeum and urodaeum) of the cloaca can only be determined through embryological studies. According to Gabe and Saint Girons (1965) it often occurs that one cloacal division gradually flows into the other, making it difficult to define exact borders for the three divisions. Certain authors, however, impose histological differences for the epithelium of the cloacal divisions (see Gabe and Saint Girons op cit.).

Gabe and Saint Girons (op cit.) observed the luminal lining of the terminal intestine of the saurians as simple, consisting of prismatic and goblet, cup-shaped cells. More recent work done by Trauth *et al.* (1987) on the cloacal anatomy of *Eumeces laticeps* shows that the coprodaeum starts as a sphincter-like structure. These authors also mention that both the intestine and coprodaeum are lined with a low to tall simple columnar epithelium. In my descriptions I used the change of epithelium, from the columnar pseudostratified epithelium of the intestine which consists of columnar and goblet cells, to a columnar pseudostratified epithelium, consisting of apical secreting cells with no goblet cells, and the presence of a sphincter-like structure as indications of the start of the coprodaeum. Like the coprodaeum, the proctodaeum in the two cordylid species examined typically starts as a sphincter-like structure. The border between the coprodaeum and the urodaeum, however, is not well delimited. In their work on *Cnemidophorus exsanguis*, Hardy and Cole (1981) mentioned that the urodaeum leads posteriorly to the proctodaeum. Gabe and Saint Girons (1965) also saw the chamber immediately anterior to the proctodaeum as the

urodaeum. Van der Merwe (1944) mentioned that the urodaeum of *Acontias meleagris* can easily be divided into two parts according to the nature of the epithelial lining: a ventral part, which can be seen as a continuation of the intestine and, a dorsal part, which stands in connection with the urogenital system. In *C. cordylus* and *P. melanotus* a much similar situation as reported for *Acontias meleagris*, was observed for the chamber immediately anterior to the proctodaeum. In these two cordylid species the ventral wall of the above mentioned chamber contains the extended epithelium of the coprodaeum while the dorsal part of the cavity contains the same epithelium as the anterior urodaeum. This phenomenon is more apparent in females because of the greater difference between the simple or pseudostratified columnar epithelium of the coprodaeum and the more stratified columnar epithelium of the urodaeum. In males, however, the epithelium of both the coprodaeum and urodaeum is simple to pseudostratified and the difference between the two epithelia is not always clear. Seen in the light of the epithelial linings of the cavity anterior to the proctodaeum, the latter mentioned chamber can be seen as a compound chamber of the coprodaeum and urodaeum. Therefore, in my description I refer to the above mentioned chamber as the coprodaeum-urodaeum cavity.

5.2. Sexual dimorphism in cloacal anatomy

The sexual differences found in *C. cordylus* and *P. melanotus*, viz. the presence of urodaeal glands in females only, dorsal (and ventral) glands which are better developed in males, and urogenital ducts which open separately into the urodaeum in females, but conjointly in males, are general observations for lizards (Gabe and Saint Girons 1965; Whiting 1969). In *Amphisbaena* (Amphisbaenidae) (Van Bedriaga 1884) and in *Lacerta agilis* (Lacertidae) (Woepke 1931), however, the ureter and the uterus on each side coalesce in females before emptying through a common duct into the cloaca. Gadow (1887)

reported that in the genus *Lophura* both ureters unite and open on one papilla on the dorsal midline. In this genus the oviducts likewise have only one opening in the cloaca, situated a little nearer to the pelvis than the urinary opening, but the two ducts are divided by a longitudinal septum which extends almost to their orifice. In contrast to *C. cordylus* and *P. melanotus* and most other reptile species, where the uteri open through the dorsal wall of the cloaca, the uteri in *Gerrhonotus multicarinatus* (Anguidae) and the snake, *Morelia spilotus* (Boidae) empty through the ventral wall of the urodaeum (Gabe and Saint Girons 1965). In contrast to the general condition where the urogenital ducts usually open conjointly into the cloaca in male lizards, the ureter and vas deferens on each side in the legless lizard, *Acontias meleagris* (Scincidae) empty separately into the cloaca (Van der Merwe 1944).

5.3. General cloacal anatomy

The general anatomy of the cloacal complex of *C. cordylus* and *P. melanotus* were found to be very similar. One difference observed was that in *P. melanotus* the anterior urodaeum stretches further to the front than in *C. cordylus*. Another difference concerns the position of the dorsal and ventral glands (see Section 5.4).

Because Cordylidae and Gerrhosauridae are sister families (sensu Lang 1991), that together with Scincidae belongs to the infraorder Scincomorpha (Estes *et al.* 1988), anatomical similarities among these taxa are to be expected (Cooper *et al.* 1992). Cooper and Trauth (1992) reported gland-like invaginations, similar to the urodaeal glands of females, for male *G. nigrolineatus*. No such invaginations were observed in any of the cordylid species, nor in *E. laticeps* (Trauth *et al.* 1987). If the species examined are taken as representative of the three families then the absence of gland-like invaginatioins must be considered the plesiomorphic state and the presence of the gland-like invaginations in males, an autapomorphy for the Gerrhosauridae.

Furthermore, in both cordylid species dorsal and ventral glands were found to be present in both males and females and these glands totally surround the proctodaeum in some regions. In females of *E. laticeps*, only dorsal glands were observed, with both dorsal and ventral glands, however, present in males (Trauth *et al.* 1987). In the latter sex the ventral glands join the bilateral dorsal glands to form a U-shaped glandular arrangement in the proctodaeal region. A similar glandular arrangement in males was observed for another scincid, *Lygosoma taeniolum* (Gabe and Saint Girons 1965). Cooper and Trauth (1992) reported that in *G. nigrolineatus* the dorsal glands start anterior to the ventral glands and that the dorsal and ventral glands completely surround the proctodaeal cavity in some regions, like in *P. melanotus* and *C. cordylus*. In *G. nigrolineatus* females, sparce dorsal and ventral glands were observed (Cooper and Trauth 1992). If representative of the families, then the possession of ventral glands by females must be seen as an synapomorphy shared by Cordylidae and Gerrhosauridae.

In *E. laticeps* and *G. nigrolineatus* the uteri empty into the urodaeal limb cavities. In all the *C. cordylus* females examined the uteri open into the coprodaeum-urodaeum cavity (urodaeum). In one *P. melanotus* female examined the one uterus opens into the urodaeal limb cavity while the other one empty into the coprodaeum-urodaeum cavity. However, in all other female *P. melanotus* specimens examined the uteri empty into the coprodaeum-urodaeum cavity.

The cloacal complex divisions of the females of the cordylid species examined differ notably from cloacal complex divisions in the following species (Gabe and Saint Girons 1965): In *Chamaeleo lateralis* (Chamaeleonidae) where the urodaeum and proctodaeum is particularly elongated; The lacertid species, *Lacerta muralis* with its remarkable elongated region anale, which is comparable with the coprodaeaum of the cordylid species examined. Also remarkable is the

elongated and S-shaped proctodaeum of this species. An S-shaped proctodaeum was also observed in *Sphenodon punctatus* (Rhynchocephalia).

Trauth *et al.* (1987) stated that in the lizard species studied thus far, no cloacal design is truly typical. They mentioned that the cloacal complex of the female *E. laticeps* is very similiar to the condition found in a female gecko (*Coleonyx variegatus*, Gabe and Saint Girons 1965), but notably different from that in a female iguanid, *Sceloporus graciosus* (Gabe and Saint Girons 1965) and from the teiid species, *Cnemidophorus exsanguis* (Trauth and Cole 1981).

According to Gabe and Saint Girons (1965) the following structures and positions in females are important to the systematical positioning: the anterior urodaeum, the position of the junctions of the uteri with the cloaca and the urinary papilla. Chamaeleonidae and *Anolis* (Iguanidae) exhibit an anterior urodaeum that is particularly long and narrow. The junction of the uteri in these species are at the anterior extremity of the urodaeal limbs. In Boidae and the Colubridae the two uteri open into the anterior extremity of the urodaeal limb cavities. In the two cordylid species examined the uteri merge into the urodaeum, posterior to where the anterior urodaeal limbs have coalesced. In the Chamaeleonidae, the ureters open directly into the urodaeum. In Boidae and Typhlopidae the urinary papillae are at the dorsal front of the urodaeum on the level of the coprodaeum sphincter, while in the cordylid species these papillae were found posteriorly to the coprodaeum sphincter, in the coprodaeum-urodaeum-coprodaeum cavity.

5.4. Cloacal glands

5.4.1. Urodaeal glands

In reptiles urodaeal glands are apparently restricted to females only (Whiting 1969). Furthermore, these glands are absent in juvenile and subadult females and probably do not appear until adulthood (Whiting op cit.). Trauth *et al.*

(1987), however, reported that in a large subadult female of the skink *Eumeces laticeps*, urodaeal glands were present, but completely regressed.

In all species examined thus far the urodaeal glands of adult females show seasonal variation which is apparently correlated with the reproductive cycle (Regamey 1935; Whiting 1969; Trauth *et al.* 1987). Regamey (1935) found that female *Lacerta agilis* exhibit well developed urodaeal glands only during the reproductive season. Trauth *et al.* (1987) likewise reported that the urodaeal glands in *Eumeces laticeps* become highly secretory during the breeding season. Cooper *et al.* (1986) established that the urodaeal glands produce a sex pheromone which stimulates courtship by conspecific males, but it is also possible that these glands may have additional non-pheromonal functions (Trauth *et al.* 1987). Regamey (1935), for example, suggested that the urodaeal glands play a role in egg laying.

As far as urodaeal glands are concerned, the two cordylid species examined, *C. cordylus* and *P. melanotus*, fit into the general picture as described above in that the urodaeal glands are present in females only. The major difference, however, is that no pronounced seasonal variation in gland activity was noted in these two species. In one gravid female *of C. cordylus* these glands were, however, completely regressed suggesting that if urodaeal gland cyclicity does occur, it is apparently asynchronous with the female breeding period. The epithelial lining of the urodaeum of both species, however, shows pronounced seasonal variation in the secretory activity of the apical mucous cells, with maximum secreting activity recorded in non-gravid females and lowest activity in gravid females. This phenomenon has not been described for any other lizard species and the significance thereof remains unknown.

In *Pseudocordylus melanotus*, males and females have asynchronous reproductive cycles (Flemming in press a,b) and mating takes place in autumn when spermiogenesis reaches a peak in males (Griffiths unpublished data). If the main function of the urodaeal gland secretions is stimulation of courtship by

conspecific males then it is to be expected that peak glandular activity will occur before the winter, coinciding with the peak of spermiogenesis in males. If the urodaeal gland also has other functions related to pregnancy or possibly, sperm storage, then glandular activity may be maintained from autumn right through the winter until birth of the young in summer. This will then explain why no apparent variation in activity of the urodaeal glands was observed between non-gravid females (collected during autumn) and gravid females (collected during late spring). The possibility also remains that gland regression may occur during winter, which would not have been detected in the present study. In *C. cordylus*, however, male and female cycles are synchronised (Jacobs unpublished data) but, like in *P. melanotus* the urodaeal glands also show little seasonal variation. It is clear that much more data are needed for a clear perspective of the functions of the urodaeal glands in cordylids. It may prove worthwhile to compare the urodaeal gland cycles of several species which follow different reproductive strategies, as this may provide additional indications of the possible functions of these glands.

5.3.2. Dorsal and ventral glands

The dorsal and ventral glands in lizards appear to be of the same complex (Disselhorst 1904; Regamey 1935; Gabe and Saint Girons 1965). Lizards may possess both dorsal and ventral glands, dorsal glands only, or neither. In *C. cordylus* and *P. melanotus* dorsal and ventral glands were found in both males and females. No seasonal variation in structure was observed in these glands in the two species examined. Trauth *et al.* (1987) reported that in contrast with the urodaeal glands the dorsal glands (and ventral glands) in the male and female *E. laticeps* show no seasonal, structural modifications but that the secretory activity of these glands increases during the reproductive season. Regamey (1935), who studied these glands in *Lacerta agilis*, also observed no variation in the glands

during the year and no relationship between their activity and the reproductive cycle could be established..

In the two cordylid species examined the dorsal and ventral glands are paired structures, dorso-lateral (dorsal glands) and ventro-lateral (ventral glands) on each side. In *Natrix natrix* the dorsal gland is paired in the male but azygous in the female (Unterhossel 1902). *Coleonyx variegatus* (Gekkonidae) and *Heloderma suspectum* (Helodermatidae) each have four dorsal gland groups (Whiting 1969). The ventral gland may be divided into two, four, six or eight distinct glandular masses (Whiting 1969).

Unterhossel (1902), Disselhorst (1904), as well as Gabe and Saint Girons (1965) reported that the dorsal glands and the ventral glands join to form a glandular ring around the proctodaeum. This condition has been observed in several species belonging to the families Agamidae, Chamaeleonidae, Gekkonidae, Lacertidae, Scincidae and Xantusiidae (Whiting 1969). In *C. cordylus* and *P. melanotus* connective tissue separates the gland tubules with muscle fibres from the inner muscularis extending among the gland tubules. Connective tissue and muscle cells also occur between the tubules in *Lacerta agilis* (Disselhorst 1904).

The distribution of serous and mucous cells in the dorsal and ventral glands varies between species and often between sexes of the same species (Gabe and Saint Girons 1965). In *C. cordylus* and *P. melanotus*, mucous cells were observed among in the epithelia of these glands. It is not certain if serous cells are also present in the epithelia of these glands. In Gekkonidae, Iguanidae, Scincidae and Xantusiidae two cell types (mucous and serous) were observed in the glands of males, while in females there were only mucous cells. In the scincids and gekkonids there is a tendency towards the concentration of mucous cells in the ventral glands and serous cells in the dorsal glands (Gabe and Saint Girons 1965). The ducts from the dorsal glands empty into the postero-dorsal wall of the proctodaeum in *C. cordylus* and *P. melanotus*. The same condition

was reported for other lizards (Whiting 1969). In a few cases the secretion of the dorsal glands appears to be discharged into the seminal groove of the hemipenis (Disselhorst 1897). In most species examined, the ventral glands open by one or more ducts into the ventrocaudal part of the proctodaeum (Whiting 1969), but in the two cordylid species the ventral glands open by more than one duct into the proctodaeum.

The specific functions of the dorsal and ventral glands are not yet known. Woepke (1931) suggested that secretions of these glands serve as a substrate for the genital products, while Lerebouillet (1851, cited in Woepke 1931) suggested that the secretions serve to keep the cloaca moist. Gabe and Saint Girons (1965) mentioned the possibility that the function of the cloacal glands may purely be mechanical, in that it may simply facilitate the moment of mating, and further the displacement the sperm cells towards the female genitals. According to Cooper and Trauth (1992) the dorsal and ventral glands may have a pheromonal activity. Trauth *et al.* (1987) hypothesized that the dorsal glands of *E. laticeps* produce a species-identifying pheromone in both sexes. Males of that species can discriminate chemical cloacal stimuli between conspecific and heterospecific males (Cooper and Garstka 1987a) and between conspecific and heterospecific females (Cooper and Vitt 1986a, b). Thus, the combined absence of the urodaeal pheromone and the presence of the species identifying pheromone of the dorsal and ventral glands in conspecifics might serve to identify male sexual competitors in skinks and also in *G. nigrolinieatus* (Cooper and Trauth 1992). The latter possible function of the gland secretions may explain why the dorsal and ventral glands are more conspicious in males.

5.5. Urinary bladder stalk

In *C. cordylus* and *P. melanotus* an urinary bladder was observed in both species. Beuchat (1986) stated that an urinary bladder is present in all amphibians and turtles, but only in some lizard species. A well developed urinary bladder is for

example present in many species of Scincimorpha, Anguinomorpha and Amphisbaenia, but in members of Gekkonidae and Iguanida it is either reduced or absent (Gabe and Saint Girons 1965). The urinary bladder is absent in all snake species investigated to date (Gabe and Saint Girons 1965). In lizards (as was also observed in the two cordylid species examined) the urinary bladder extends ventrally from the cloaca and is in contact with it by means of a bladder stalk (Mulaik 1946). In the two cordylid species examined this junction with the cloaca is at appoximately the same level where the coprodaeum and the anterior urodaeum merge.

It was reported that both the urinary bladder and the cloaca can serve as storage sites for urine which can be modified or reabsorbed as the animals dehydrate (Dantzler and Scmidt-Nielsen 1966; Minnich 1982; Beuchat, Vleck and Braun 1986). There is evidence that the urinary bladder may have an osmoregulatory function in neonatal *Sceloporus jarravi* (Beuchat *et al.* 1986) and the sand dune lizard, *Aporosauria anchietae* (Beuchat, Braun and Vleck 1985). Gelatinous urine is frequently found in the urinary bladder of dehydrated tortoises and lizards (Rogers 1966; Minnich 1979). Van Wyk (pers. comm.) has found a gelatinous substance in the bladder of the cordylid species, *Cordylus giganteus* on many occasions. Bolten and Beuchat (1991) stated that because the urine of terrestrial reptiles contains urate in solution, both the cloaca and the bladder can serve as sites for significant urate precipitation as water is removed from the urine.

The presence of ciliated cells in the urinary bladder stalk of the two cordylid species examined are in line with results reported for eight lizard species examined by Bolton and Beuchat (1991). The function of these ciliated cells in the urinary bladder stalks of lizards is not yet known. Bolton and Beuchat (1991) suggested that the cilia may play a role in transferring particulate matter such as urate from the bladder into the cloaca.

5.6. Sperm storage structures

In *P. melanotus*, male and female reproductive activity occur asynchronously in that spermiogenesis in males reaches a peak in autumn while ovulation in females only occurs in early spring (Flemming in press a,b). Griffiths (unpublished data) observed mating in late autumn only, suggesting that sperm are stored by females until spring. In *Cordylus giganteus* sperm are stored in the ductus epidydimus and in the vas deferentia from autumn to December (Van Wyk pers. comm). In the male cordylid species examined, the sperm are probably also stored in the vasa deferentia in *P. melanotus*. It seems as if sperm storage in the females are not needed. Among the lacertids and a number of iguanids, it has been found that the sperm are stored in females in a flattened expansion of the utero-vaginal region just anterior to the cloaca. Certain members of the Chamaelonidae and the Iguanida (genus *Anolis*) have true seminal receptacles in the form of fingerlike tubes attached to the chorion of the uterus (oviduct) (Saint Girons 1962; Fox 1963). Hardy and Cole (1981) reported seminal receptacle-like structures at each edge of the uteri in *Cnemidophorus exsanguis* but they found no sperm cells present.

Robb (1965) reported "cloacal pouches" in the mid-dorsal wall of the proctodaeum in male Australian typhlopids (for example: *Typhlops ligatus* and *T. proximus*). Robb suggested that because of the structure (non-glandular epithelial lining) and position of the these pouches relative to the other parts of the reproductive system it may be sperm sacs. During copulation sharp contraction of the muscular walls of the pouches would presumably force the seminal fluid into the seminal groove and along it into the oviduct of the female (Robb 1965).

5.7. Intestinal- and urogenital products

The faeces are probably stored in the terminal portion of the intestine with the musculature in the walls of the proctodaeum facilitating the evacuation of the

faecal pellets. The formation of faecal pellets in the coprodaeum-urodaeum cavity may cause mingling of the sperm cells with the faeces or blockage of the sperm during copulation. The coprodaeum sphincter may serve to close the entrance to the cloaca and by so doing prevent the above mentioned problem. Where the coprodaeum and the urodaeum join there must be a mechanism preventing mingling of the faeces with urate and urine and in the case of males with sperm cells. It was observed that the last part of the faecal pellet when evacuated is covered by a white cap of solid urate. This indicates that urate in a solid form is stored in the cloaca which is always available during faecel evacuation. Histological examination of the cloacal divisions showed no specialized structures for urate storage. Therefore, this solid urate must be stored in the coprodaeum-urodaeum cavity or in the ureters. Because the solid urate cap does not appear in the front of the faecel pellet it can be assumed that it is not stored in the digestive tract, which leaves us with the ureters. However, because the vasa deferentia and the ureters unite anterior to their junction with the cloaca, storage of solid urate in the terminal part of the ureter may block sperm evacuation during mating. It is therefore possible that the solid urate is stored higher up in the ureters and that there exist an mechanism for the solid urate to be forced out during faecal evacuation. In contrast with the ureter the terminal part of the vas deferens possesses a relatively well developed circularly arranged muscle fibre layer. This muscle layer may facilitate the sperm evacuation during copulation or closure of this duct if necessary.

The function of the secretions observed among the sperm cells in the males of both species is not clear. Gabe and Saint Girons (1965) mentioned that the spermatozoa are covered by secretions from the epididymis. Intensively staining secretions were observed in the tubules of the kidneys and in the anterior ureters of the males which probably represents the sexual segment of the kidney. The sexual segment of the kidney in males is androgen dependent and undergoes a seasonal cycle of secretory activity corresponding to the

spermatogenic cycle (Prasad and Reddy 1972). Bradshaw (1986) stated that the sexual segment is thought to play a similar role than the seminal vesicles and prostate gland of mammals, capacitating sperm and providing nutrients during sperm storage (Cueller *et al.* 1972).

5.8 Facilitation of copulation

In the frog *Ascaphus* (De Villiers 1934) and in the legless lizard, *Acontias meleagris* (V.d. Merwe 1944) dorsal and ventral "gliding surfaces" in the cloacal wall were observed. These "gliding surfaces" are regions where the connective tissue of the cloaca is separated from the adjacent muscularis. The function of these "gliding surfaces" is not certain but it may have a role to play during copulation (Van der Merwe 1944). Van der Merwe mentioned that the ventral part of the cloaca will be pushed backwards during copulation and that a "gliding surface" in this area will be required. The connective tissue ventral to the ventral glands, just dorsal to the hypoischium in *C. cordylus* and *P. melanotus*, which stretches from the vent to approximately the start of the proctodaeum, may have a similar purpose as the ventral "gliding surface" as suggested for *A. meleagris* by Van der Merwe (1944).

SUMMARY

1. The macro- and microanatomy of the cloacal complex of the Drakensberg crag lizard, *Pseudocordylus melanotus* and the Cape girdled lizard, *Cordylus cordylus*, both members of the family Cordylidae, were described and compared with that of other reptiles (mainly lizards). Animals in different reproductive conditions were used to establish seasonal variation in cloacal anatomy.

2. As is typical of reptiles, the cloaca of the two species examined can be divided into three subdivisions: the coprodaeum, the urodaeum and the proctodaeum. The coprodaeum receives the intestine, the urodaeum receives the urogenital ducts and the proctodaeum leads to the exterior.

3. In both cordylid species a urinary bladder extends ventrally from the coprodaeum-urodaeum part of the cloaca and is in contact with it by means of a urinary bladder stalk. The urinary bladder stalk contains ciliated and non-ciliated epithelial cells, but near its junction with the cloaca primarily consists of non-ciliated cells. The ciliated cells in the bladder stalk may play a role in transferring particulate matter such as urate from the urinary bladder into the cloaca.

4. From the intestine to the coprodaeum, the epithelium changes from a columnar epithelium with goblet cells to a columnar epithelium consisting of mucous secreting cells only. The border between the coprodaeum and the urodaeum is not well delimited. Where the coprodaeum and the urodaeum unite, a cavity (coprodaeum-urodaeum cavity) is formed which contains the dorsal epithelium of the anterior urodaeum and the ventral epithelium of the coprodaeum.

5. In both sexes the epithelium of the coprodaeum and the proctodaeum and also the urodaeum in males is typically columnar, 1-2 cell rows in thickness. In females, however, the urodaeal epithelium may vary from 2-7 cell rows in thickness. The epithelium of the proctodaeum changes from a simple- or pseudostratified columnar one to a stratified squamous one which become cornified near the vent.

6. External to the mucosa of the cloacal divisions are an inner- and an outer muscularis which are separated by a connective tissue layer. The inner muscularis consists of circular and longitudinal muscle fibres of which the thickness can vary anteriorly to posteriorly. In contrast, the outer muscularis consists only of longitudinal smooth muscle fibre groups which show little variation in thickness. External to the muscularis is a layer of connective tissue (serosa).

7. The start of the coprodaeum and the proctodaeum in the two cordylid species examined is marked by a sphincter-like structure, with a well developed inner muscularis consisting primarily of circularly arranged smooth muscle fibres. From anterior to posterior the inner muscularis of the proctodaeum become reduced and near the vent is lacking.

8. Two types of cloacal glands were observed in the cordylid species. The urodaeal glands are only found in the urodaeal walls of the females. These glands are tubular, branched and exocrine and contains mucous cells. Dorsal and ventral glands are branched, tubular and exocrine. It is not certain if both mucous and serous cells are present in these glands. These glands are located dorso-lateral (dorsal glands) and ventro-lateral (ventral glands) to the proctodaeum. In both cordylid species examined, both dorsal and ventral glands were found present in both sexes but the glands were more prominent in the

males. In both sexes of *C. cordylus* and in the males of *P. melanotus* dorsal glands extended further posteriorly than do the ventral glands. However, in *P. melanotus* females, the ventral glands extended further backwards than the dorsal glands.

9. A relatively thick connective tissue layer was observed ventrally between the proctodaeum and the hypoischium (innervated by skeleton muscles). This connective tissue layer may facilitate the backwards push of the cloaca during copulation.

10. In the two cordylid species examined, the main sexual differences were associated with the urodaeum. In females the urodaeal wall, especially the dorsal wall, exhibits large folds, which are absent or reduced in males. Furthermore, in females the urogenital ducts (uteri and ureters) open separately into the urodaeal cavity- the uteri more anterior than do the ureters. In males, however, the urogenital ducts (vasa deferentia and ureters) unite before opening conjointly into the cloaca.

11. The anterior part of each vas deferens is surrounded by a relatively thin layer of circularly arranged smooth muscle fibre, which become thicker near its connection with the ureter on each side. This terminal muscle layer may surrounded by a well developed layer of circularly arranged smooth muscle fibres. The epithelium of the ureter in both sexes changes from non-secretory anteriorly to mucous secretory posteriorly.

12. The luminal epithelium of the urodaeum show seasonal variation in secretory activity. In the females of both cordylid species examined, the secreting activity of the urodaeal lining was reduced in gravid females. In one gravid *C. cordylus* female the urodaeal glands were more or less totally regressed. However, in the other females examined, the urodaeal glands show

no pronounched seasonal variation in secretory activity. Furthermore, the intestine epithelium showed variation in the height, but is not certain if it is a seasonal variation or the result of intraspecific variation. No apparent seasonal variation in secreting activity of the dorsal and ventral glands were observed.

13. Intraspecific variations were found in both species. These variations include: the type of the anterior junction between the urinary bladder stalk with the cloaca (laterally or medially), the junction of the urinary bladder stalk with the coprodaeum, urodaeum or the terminal part of the intestine and the position of the uteri junctions with the urodaeum.

14. The cloacal complex anatomy of both sexes of the two cordylid species shows great similarity. In *P. melanotus* the urodaeal limbs showed the tendency to extend more anteriorly than in *C. cordylus*. To determine if the cloacal complex anatomy can be useful as an additional character for the determination of phylogenetic relationships among the cordylid genera more cordylid species should be examined.

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